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Revision of the Sauropterygian Reptile Genus *Cymatosaurus* v. Fritsch, 1894, and the Relationships of *Germanosaurus* Nopcsa, 1928, from the Middle Triassic of Europe

Olivier Rieppel

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Revision of the Sauropterygian Reptile Genus *Cymatosaurus* v. Fritsch, 1894, and the Relationships of *Germanosaurus* Nopcsa, 1928, from the Middle Triassic of Europe

Olivier Rieppel

Abstract

Three species are currently recognized within the genus *Cymatosaurus* from the late Scythian and early Anisian of Europe, viz. *Cymatosaurus fridericianus* v. Fritsch, 1894, *Cymatosaurus latifrons* Gürich, 1884, and *Cymatosaurus multidentatus* (F.v. Huene, 1958). All other previously described species of *Cymatosaurus* are considered either junior synonyms of *Cymatosaurus latifrons* (*C. gracilis* Schrammen, 1899; *C. silesiacus* Schrammen, 1899) or a nomen dubium (*C. erythreus* E.v. Huene, 1944). *Germanosaurus schafferi* Arthaber, 1924, is recognized as a separate genus and species within the Nothosauridae, sister-group of the Nothosaurinae (including *Nothosaurus* and the *Silvestrosaurus–Ceresiosaurus–Lariosaurus* clade). *Germanosaurus* (*Eurysaurus*) *latissimus* (Gürich, 1891) is treated as a nomen dubium. A cladistic analysis based on the critical revision of the genera *Cymatosaurus* and *Germanosaurus* improves resolution among Triassic stem-group Eosauropterygia. The resulting cladogram is used as the basis for a comparison of phylogenetic pattern and stratigraphic distribution of the Sauropterygia.

Zusammenfassung

Innerhalb der Gattung *Cymatosaurus* aus dem obersten Skyth und unteren Anis Europas werden gegenwärtig drei Arten als gültig anerkannt: *Cymatosaurus fridericianus* v. Fritsch, 1894, *Cymatosaurus latifrons* Gürich, 1884, und *Cymatosaurus multidentatus* (F.v. Huene, 1958). Alle anderen beschriebenen Arten von *Cymatosaurus* sind entweder jüngere Synonyme von *Cymatosaurus latifrons* (*C. gracilis* Schrammen, 1899; *C. silesiacus* Schrammen, 1899) oder ein nomen dubium (*C. erythreus* E.v. Huene, 1944). *Germanosaurus schafferi* Arthaber, 1924, wird als selbtändige Gattung und Art innerhalb der Nothosauridae anerkannt, die die Schwestergruppe der Nothosaurinae (*Nothosaurus, "Silvestrosaurus," "Ceresiosaurus,"* und *Lariosaurus*) repräsentiert. *Germanosaurus* (*Eurysaurus*) *latissimus* (Gürich, 1891) ist ein nomen dubium. Eine kladistische Analyse, die auf der kritischen Revision der Gattungen *Cymatosaurus* and *Germanosaurus* fusst, resultiert in einem besseren Verständnis der Verwandtschaftsverhältnisse unter triassischen Eosauropterygiern. Auf der Grundlage dieser Analyse wird das Muster der Verwandtschaftsbeziehungen mit dem Muster der stratigraphischen Verbreitung der Sauropterygia verglichen und diskutiert.

Introduction

The genus *Cymatosaurus* was erected by Fritsch (1894) for an isolated, dorsoventrally flattened skull (and an isolated snout fragment) collected in the lowermost Muschelkalk (mu_1, lower Anisian) exposed in the quarries of the "Portland-Cement-Fabrik" at Halle/Saale, Germany. Fritsch

(1894) recognized many similarities that the specimen shares with *Nothosaurus*, but it differs from the latter genus in having strongly reduced nasals, a trait that *Cymatosaurus* shares with *Pistosaurus* from the upper Muschelkalk (mo_1) of Bayreuth (Bavaria).

Sauropterygia of equivalent or slightly older age (mu_1, lowermost Muschelkalk) had previously been collected in the Gogolin beds of Upper Silesia, and isolated skulls from those deposits had been described as *Nothosaurus latifrons* Gürich, 1884, or *Nothosaurus latissimus* Gürich, 1891, respectively. Fritsch (1894) did not refer to Gürich's (1884, 1891) material, although in his review of the genus *Nothosaurus* Koken (1893) had suggested that Gürich's (1891) species might be referred to a different genus. Schrammen (1899) reviewed the nothosaurs from the lower Muschelkalk of Upper Silesia, referred both of Gürich's species to the genus *Cymatosaurus*, and described two new species, viz. *Cymatosaurus gracilis* and *C. silesiacus*. Morphological comparison led him to conclude that *Cymatosaurus* must be close to the common ancestor of *Nothosaurus* and *Pistosaurus*.

Frech (1903) erected the new subgenus *Eurysaurus* to include *Cymatosaurus latissimus*, which he found to be intermediate between *Cymatosaurus* and *Nothosaurus*: the frontals are paired and the nasals reduced in *Eurysaurus latissimus* as in *Cymatosaurus*, but the reduced nasals still reach the posterior margin of the external naris as in *Nothosaurus*. Nopcsa (1928a, p. 21, 1928b, p. 173) replaced the genus name *Eurysaurus* by *Germanosaurus* because the first name was preoccupied. This had escaped Arthaber (1924), who in his review of nothosaurs retained *Eurysaurus* as a subgenus of *Cymatosaurus* and described a new species, *Eurysaurus schafferi*, from the lowermost Muschelkalk (mu_1, Gogolin beds) of Gogolin, Upper Silesia.

The genus *Cymatosaurus* was comprehensively reviewed by E.v. Huene (1944), who described another species, *Cymatosaurus erythreus*, from the upper Buntsandstein (so_2, Röt) of Rüdersdorf near Berlin, the earliest representative of its genus in the Germanic Triassic. E.v. Huene (1944) retained *Germanosaurus* as a subgenus, to which she referred the species *gracilis* Schrammen, *latissimus* Gürich, *schafferi* Arthaber, and *silesiacus* Schrammen; *Cymatosaurus ss.* would include the species *erythreus* E.v. Huene, *fridericianus* Fritsch, and *latifrons* Gürich.

Jaekel (1911, p. 148, Fig. 161; this specimen can no longer be located today) figured a skull from the lower Muschelkalk of Mühlhausen (Thuringia), which he referred to "*Nothosaurus* (*Cymatosaurus*) cf. *fridericianus*." This skull is clearly that of *Nothosaurus marchicus* (Rieppel & Wild, 1996), as is indicated by its proportions (relatively short rostrum, relatively small upper temporal fossae, maxillary tooth row not extending up to the midpoint of the upper temporal fossa), the well-developed nasals, the fused frontals, and the relatively forward position of the pineal foramen (see also Schröder, 1914, p. 73).

Huene (1958) described a new species of the pachypleurosaur genus *Anarosaurus* Dames, 1890, from the lower Anisian of the Lechtaler Alps (Austria), *Anarosaurus multidentatus*. Redescription of the holotype resulted in its identification as *Cymatosaurus* (Rieppel, 1995c), indicating that the genus had expanded from the Muschelkalk Basin and reached the Alpine Triassic during early Anisian times (Rieppel & Hagdorn, 1996). Throughout the Germanic and Alpine Triassic, the genus *Cymatosaurus* remains restricted to the lower Muschelkalk and lower Anisian respectively. Productive deposits (*orbicularis* beds, basal middle Muschelkalk) of Esperstädt, Jena, Querfurt, and Rüdersdorf have yielded abundant material of *Nothosaurus* (Rieppel & Wild, 1996), but not a single diagnostic skull fragment of *Cymatosaurus*.

Analysis of the invertebrate fauna from lower Muschelkalk deposits in the eastern part of the Germanic Basin shows strong Asiatic affinities and indicates that these taxa reached the Muschelkalk Basin from the Paleotethys through the East Carpathian gate (Kozur, 1974; Hagdorn, 1985; Urlichs & Mundlos, 1985). In view of this paleobiogeographical context, it is interesting to note that the only possible *Cymatosaurus* described from outside Europe is *Micronothosaurus stensioei* Haas, 1963, from the upper Muschelkalk of Wadi Ramon, Israel. The specimen differs from *Nothosaurus* in a number of characteristics, such as the relatively forward position of the pineal foramen, the distinct posterolateral lappets of the frontal approaching the pineal foramen, a narrow postorbital bridge, relatively small upper temporal fenestrae compared to the size of the orbits, no evidence for a posterior extension of the tooth row beyond the posterior margin of the orbit, and a poorly ossified occiput with large posterior openings for the cranioquadrate passage. Unfortunately, some morphological details remain obscure in Haas's (1963) description, such as the paired or unpaired condition of the frontal and the relations of the jugal and postorbital along the posterior margin of the orbit. In view of the many shared similarities, Schultze (1970) identified *Micronothosaurus stensioei* as a cymatosauroid, possibly even belonging to the genus *Cymatosaurus*. If this identification is valid, and if Haas's (1963) indication of its stratigraphic occurrence in the upper Muschelkalk is correct, the specimen would significantly expand the geological occurrence of the genus *Cymatosaurus* beyond the central and western European occurrences into the uppermost Anisian or lower Ladinian.

In fact, Haas (1963, p. 161) specifies that the specimen came from "Brotzen's layer D2 (*Ceratites* beds)," but "*Nothosaurus* or related genera" are cited by Brotzen (1957, p. 202) as coming from the *Ceratites* zone D1. The overlying *Ceratites* zone D2 was correlated by Brotzen (1957) with the *Trinodosus* zone, and both zones (D1 and D2) were considered equivalent to the Alpine upper Anisian (Brotzen, 1957, p. 206). More recent analyses equate the *Trinodosus* zone of the Tethyan province with the lower Illyr, of lower upper Anisian age, which corresponds to the upper lower Muschelkalk (mu_2) (Rieber, 1973; Bucher, 1988; Budurov et al., 1993; Brack & Rieber, 1993). Although geologically younger than the occurrence of *Cymatosaurus* in the Gogolin beds of Upper Silesia, the Israel cymatosauroid still is in deposits equivalent to the lower Muschelkalk.

Institutional abbreviations are as follows: BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin; Ha, Institut für Geowissenschaften, Martin-Luther-Universität, Halle/Saale; Mbg, Fachbereich Geowissenschaften, Philipps Universität, Marburg/Lahn; NHMW, Naturhistorisches Museum, Wien; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

Systematic Paleontology

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994a

Cymatosauridae Huene, 1948

Definition—A monophyletic taxon including the genus *Cymatosaurus*.

Diagnosis—Small to large eosauropterygians with a moderately depressed skull; snout constricted; postorbital skull distinctly elongated; occiput deeply concave; supraoccipital vertically oriented and in loose connection with the dermatocranium; distinctly reduced nasals that may or may not enter the external naris; frontals paired; posterolateral processes of frontals closely approach upper temporal fossa and may enter its anteromedial margin; parietals incompletely or completely fused; jugal enters posterior margin of the orbit and remains excluded from upper temporal arch; quadratojugal absent.

Distribution—Uppermost Buntsandstein and lower Muschelkalk, lower Anisian, Middle Triassic, Europe and ?Israel.

Comments—The cladistic analysis discussed below indicates a sister-group relationship of *Cymatosaurus* and *Pistosaurus*, with *Corosaurus* representing the sister-taxon of the former two. An argument could therefore be made that the latter two genera be included in the Cymatosauridae. This conclusion is not formalized here, because the addition of plesiosaurs and pliosaurs to the analysis may show *Pistosaurus* to be the sister-taxon of plesio- and pliosaurs (see Sues, 1987; Storrs, 1991, 1993b). The results reported here support the concept of the Pistosauria proposed by Edinger (1935; see also Sanz, 1983; Alafont & Sanz, 1996), to include *Cymatosaurus, Pistosaurus,* and, by extension, plesio- and pliosaurs. The Pistosauria may have to be extended to include *Corosaurus,* or a new higher taxon may have to be named to include *Corosaurus* and the Pistosauria.

Cymatosaurus v. Fritsch, 1894

1884	*Nothosaurus,* Gürich, p. 132, Pl. II, Figs. 2–4
1891	*Nothosaurus,* Gürich, p. 967, Fig. on p. 968.
1894	*Cymatosaurus,* v. Fritsch, p. 10
1903	*Eurysaurus,* Frech, p. 15.
1928a	*Cymatosaurus,* Nopcsa, p. 44
1928b	*Cymatosaurus,* Nopcsa, p. 173.
1944	*Cymatosaurus* (*Germanosaurus*) (partim), E.v. Huene, p. 208.

Type Species—*Cymatosaurus fridericianus* v. Fritsch, 1894, from the lower Muschelkalk (lower Middle Triassic), Halle/Saale, Germany.

Definition—A monophyletic taxon including the species *fridericianus, latifrons,* and *multidentatus.*

DIAGNOSIS—Same as for family, of which this is the only genus.

DISTRIBUTION—Same as for family, of which this is the only genus.

COMMENTS—*Lamprosauroides goepperti* (Meyer, 1860; *Lamprosauroides* replaces *Lamprosaurus*: K. P. Schmidt, 1927, p. 58) was considered a cymatosauroid by Schrammen (1899, p. 408). In view of its fragmentary nature, *Lamprosauroides goepperti* (Meyer, 1860) remains a nomen dubium (Rieppel, 1995a).

Cymatosaurus fridericianus v. Fritsch, 1894

1894	*Cymatosaurus fridericianus,* v. Fritsch, p. 281 *ff.,* Pl. 16, Fig. 1; Pl. 17, Pl. 18, Figs. 1–12.
1899	*Cymatosaurus fridericianus,* Schrammen, p. 389 *ff.,* Pl. 24, Figs. 5a–c.
1914	*Cymatosaurus fridericianus, Schröder,* p. 78 *ff.,* Figs. 15, 21.
1924	*Cymatosaurus fridericianus,* Arthaber, p. 475, Figs. 10a–b.
1928	*Cymatosaurus fridericianus,* Schmidt, p. 393, Fig. 1105.
1934	*Cymatosaurus fridericianus,* Kuhn, p. 42.
1944	*Cymatosaurus fridericianus,* E.v. Huene, pp. 198 *f,* 207 *f.*
1964	*Cymatosaurus fridericianus,* Kuhn, p. 12
1983	*Cymatosaurus fridericianus,* Sanz, Fig. 1b.
1995c	*Cymatosaurus fridericianus,* Rieppel, p. 295, Figs. 8A–B.

HOLOTYPE—Skull (Ha, uncatalogued; Figs. 1, 2).

LOCUS TYPICUS—Lower Muschelkalk (mu_1), Halle/Saale, Germany.

DIAGNOSIS—A species of *Cymatosaurus* of large size (tip of snout to back end of parietal skull table up to 200 mm); three maxillary teeth preceding paired maxillary fangs; nasals reduced, excluded from external naris; prefrontal and postfrontal in contact at dorsal margin of orbit; frontal enters anterior margin of upper temporal fossa.

DISTRIBUTION—Lower Muschelkalk (lower Anisian, lower Middle Triassic), central Europe.

REFERRED SPECIMENS—BGR S 44/3: a small and incomplete skull from the lower Muschelkalk (Gogolin Beds, mu_1) of Gogolin, Upper Silesia Rieppel, 1994a, Fig. 39). The fragment represents the posterior part of the dermatocranium, from which most of the braincase has dropped out (Fig. 3). This indicates incomplete ossification and hence possibly a juvenile status of the specimen (but see further discussion below). The frontal enters the anteromedial margin of the upper temporal fossa, a derived feature shared with the holotype of *Cymatosaurus fridericianus.* The specimen is therefore interpreted as a juvenile representative of the latter species.

The snout fragment from the lower Muschelkalk of Halle referred to *Cymatosaurus* sp. by Fritsch (1894, p. 300, Pl. 16, Fig. 2) is not diagnostic at the species level but differs from *Cymatosaurus fridericianus* only by its somewhat smaller size. The specimen can no longer be located today. A similar snout fragment (SMNS 7209; Fig. 4) is known from the lower Muschelkalk (mu_1) of Freudenstadt.

MORPHOLOGICAL DESCRIPTION—*C. fridericianus* is characterized by a relatively long and slender skull with a pronounced rostrum (Fig. 2). The occipital condyle is not preserved. Skull length from the tip of the snout to the posterior end of the parietal skull table is 195 mm, the length from the tip of the snout to the mandibular condyle of the quadrate approximately 238 mm. The occiput is deeply excavated, the mandibular articulations located well behind the assumed level of the occipital condyle. The external nares are almost twice as long as they are broad, and the upper temporal fossa is relatively somewhat smaller than in *Nothosaurus.* Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of 1.64 (1.2–2.5 in *Nothosaurus*). Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 1.87 (1.5–2.0 in *Nothosaurus*). Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external nares yields a ratio of 2.68 (2.3–3.4 in *Nothosaurus*). Dividing the longitudinal diameter of the external naris by its transverse diameter yields a ratio of 1.94 (the corresponding ratio varies from 1.0 to 2.2 in *Nothosaurus,* depending on the species). Dividing the longitudinal diameter of the upper temporal fossa by the longitudinal diameter of the orbit yields values of 1.76 (left side) and 1.96 (right side), respectively (the corresponding ratio varies from 2.1 to 3.9 in *Notho-*

saurus, with *N. marchicus* at the lower end and *N. mirabilis* at the upper end of that range).

The relatively long and slender rostrum, formed by the paired premaxillae, is distinctly set off from the bulging maxillaries by a rostral constriction. The premaxillary–maxillary suture is located at the anterolateral corner of the external naris. Broad posterior (nasal) processes of the premaxilla separate the external nares from one another and meet the paired frontals in an interdigitating suture at the level of the anterior margin of the orbit. Between the external nares and the orbits, the maxilla is broadened to accommodate the roots of the paired maxillary fangs. The nasals are small, splint-like bones whose posterior tip reaches the level of the anterior margin of the orbit, but which remain excluded from the posterior margin of the external naris. The lacrimal is lacking. The prefrontal is relatively larger than in *Nothosaurus,* located at the anterodorsal corner of the orbit, and it meets the postfrontal along the dorsal margin of the orbit. The postfrontal is a large element defining the posterodorsal margin of the orbit as well as the anterior margin of the upper temporal fossa. The postorbital bridge is relatively narrower than in *Nothosaurus.* Dividing the width of the postorbital bridge by the width of the maxilla between the external naris and the anterior margin of the orbit yields a value of 0.36 for *C. fridericianus*; the corresponding ratio varies from 0.8 to 1.8 in *Nothosaurus* (depending on the species).

The frontals are large, paired elements that meet the fused parietal at a level somewhat behind the anterior margin of the upper temporal fossa. Unlike any specimens of *Nothosaurus* (and some skulls of *Cymatosaurus* [see below]), the frontal enters the anteromedial margin of the upper temporal fossa. The parietal is a narrow element with the pineal foramen located slightly anterior to its midpoint. The suture between squamosal and parietal at the posterior margin of the upper temporal fossa cannot be identified unequivocally. The squamosal meets the postorbital in an overlapping suture within the upper temporal arch; the anterior tip of the squamosal lies behind the level of the anterior margin of the upper temporal fossa. The precise shape and relations of the jugal bone, located at the posteroventral margin of the orbit, cannot be identified. It did not, however, extend into the upper temporal arch, approaching the anterior tip of the squamosal.

The ventral view of the skull discloses a large fontanelle between the premaxillae, enlarged by separation of the premaxillae due to dorsoventral compression of the skull. The premaxillary rostrum carries five tooth positions on each side; replacement pits are distinctly elongated and drop-shaped, located posteromedial to the functional tooth positions. Three small maxillary teeth precede the paired maxillary fangs. The total count of maxillary teeth cannot be established. The vomers are paired elements that meet the maxillae at the anterior margin of the internal nares, thus excluding the premaxillae from the latter. The posterior margin of the internal nares is defined by the palatines. The internal nares are relatively broad and short: division of their longitudinal diameter by their transverse diameter yields a ratio of 2.1; corresponding values vary from 1.28 to 3.86 in *Nothosaurus,* with *N. marchicus* at the lower end and *N. mirabilis* at the upper end of that range. As compared to *Nothosaurus,* the internal nares are positioned somewhat farther back relative to the external nares (Table 1).

The vomers meet the anterior tips of the pterygoids in a transversely oriented interdigitating suture behind the level of the posterior margins of the internal naris. The ectopterygoid is a relatively short and broad element located at the anterior margin of the subtemporal fossa, and it forms a well-developed (ecto-)pterygoid flange for the origin of the superficial pterygoideus muscle. The quadrate ramus of the pterygoid is well preserved on the right side of the skull and (as in *Nothosaurus*) shows well-developed flanges at both its medial and lateral edges for the origin of the deep pterygoideus muscle.

Discussion—Among all described species of *Cymatosaurus,* the frontal approaches the anteromedial margin of the upper temporal fossa to a variable degree. Only in *Cymatosaurus fridericianus* does the frontal enter the upper temporal fossa and participate in the formation of the ventrally descending flange from which originate deep fibers of the jaw adductor muscles. Unlike in *Cymatosaurus latifrons,* three (rather than one) small maxillary teeth precede the maxillary fangs—the plesiomorphic condition compared to the outgroup (Nothosauridae: Rieppel, 1994b). The degree of reduction of the nasals (entering external nares or excluded therefrom), as well as the presence or absence of a contact between prefrontal and postfrontal along the dorsal margin of the orbit, is highly variable among all the specimens of *Cymatosaurus* ever described, and these characters cannot be used to differentiate separate species within the genus.

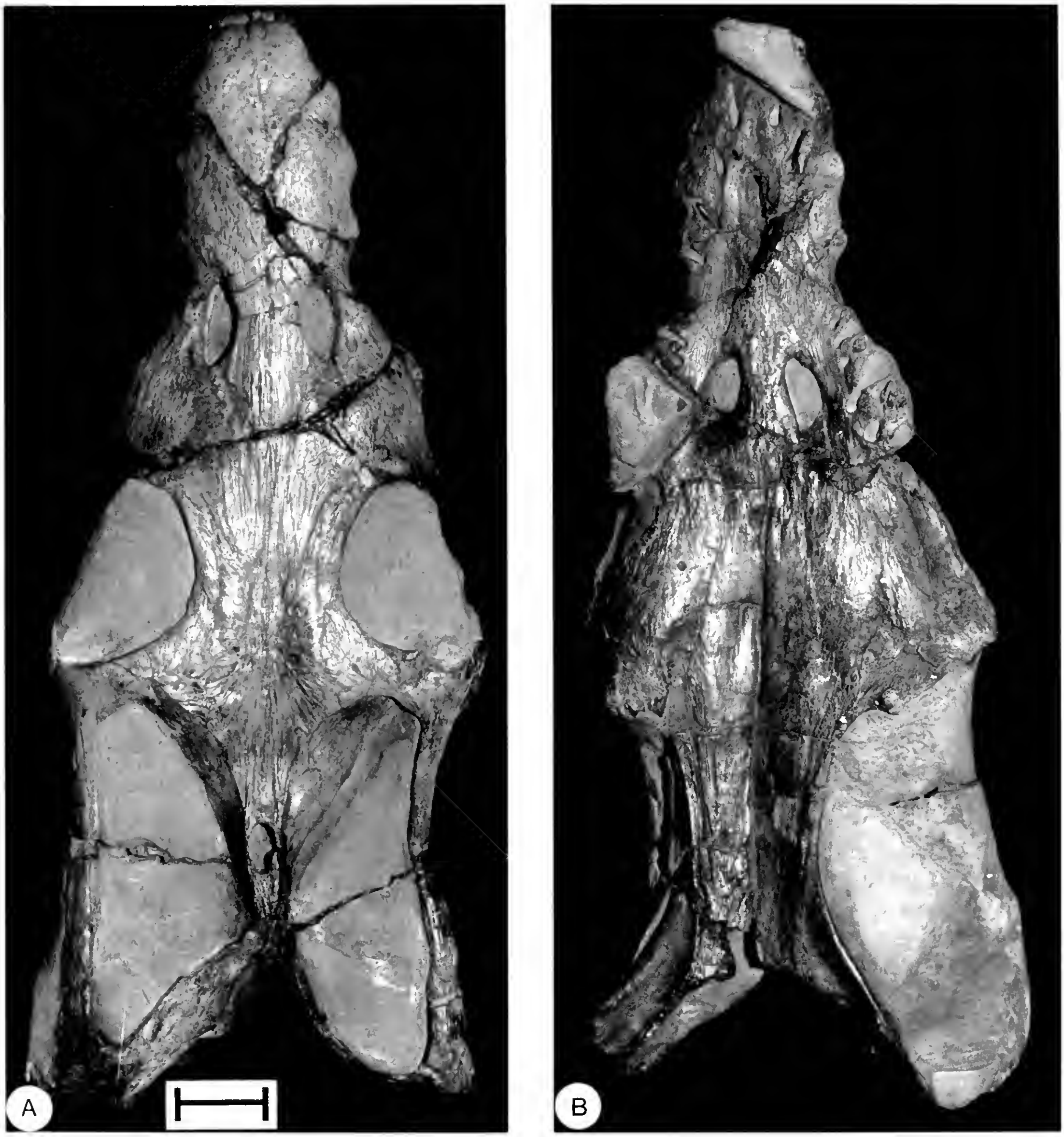

FIG. 1. The skull of the holotype of *Cymatosaurus fridericianus* v. Fritsch, 1894 (Ha, uncatalogued), from the lower Muschelkalk of Halle/Saale. **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm.

***Cymatosaurus latifrons* (Gürich, 1884)**

1884	*Nothosaurus latifrons,* Gürich, p. 132, Pl. 2, Figs. 3–4.
1893	*Nothosaurus latifrons,* Koken, p. 366 *ff.,* Figs. 4–5.
1899	*Cymatosaurus* (*Nothosaurus*) *latifrons,* Schrammen, p. 388 *f.*
1899	*Cymatosaurus gracilis,* Schrammen, p. 402, Pl. 23, Figs. 2–3; Pl. 25, Figs. 6a–b, 7.
1899	*Cymatosaurus silesiacus,* Schrammen, p. 402, Pl. 21, Pl. 22, Figs. 1–2; Pl. 25. Figs. 3a–e; Pl. 26, Figs. 1–3.
1903	*Cymatosaurus gracilis,* Frech, p. 15.
1903	*Cymatosaurus latifrons,* Frech, Figs. 2a–c.

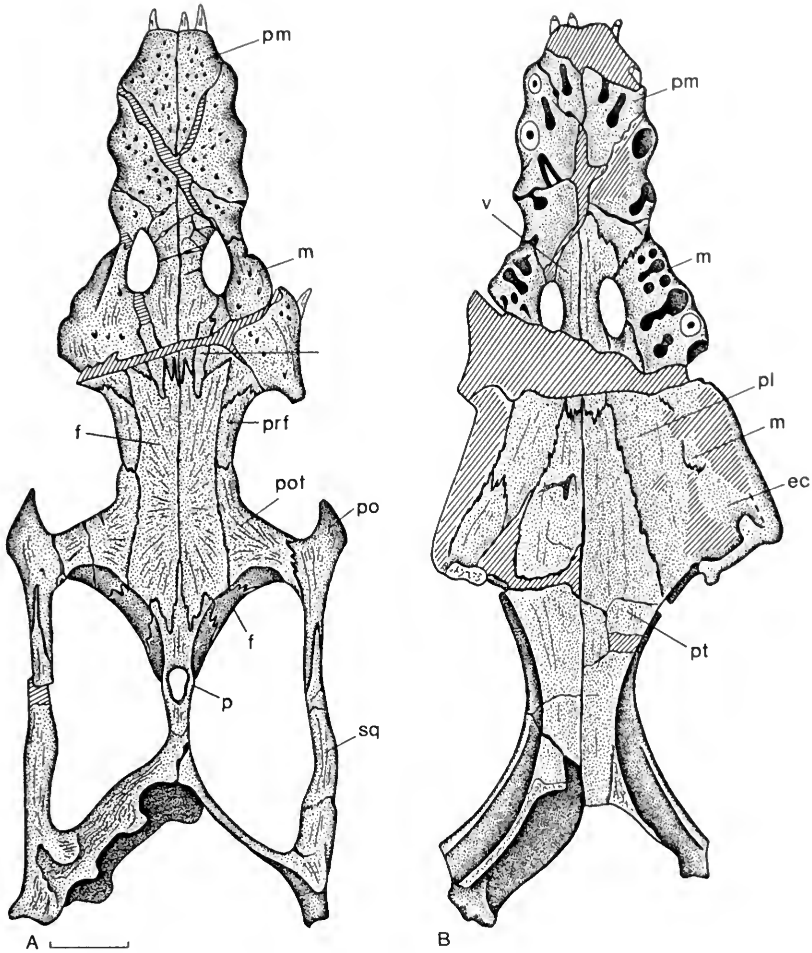

FIG. 2. The skull of the holotype of *Cymatosaurus fridericianus* v. Fritsch, 1894 (Ha, uncatalogued), from the lower Muschelkalk of Halle/Saale. **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm. Abbreviations: ec, ectopterygoid; f, frontal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; sq, squamosal; v, vomer.

1903 *Cymatosaurus silesiacus,* Frech, p. 15.
1914 *Cymatosaurus gracilis,* Schröder, p. 78 *ff.*, Fig. 16.
1914 *Cymatosaurus latifrons,* Schröder, p. 86 *ff.*
1914 *Cymatosaurus silesiacus,* Schröder, p. 82 *ff.*
1924 *Nothosaurus latifrous,* Arthaber, p. 476.
1924 *Eurysaurus latifrous,* Arthaber, p. 477.
1924 *Cymatosaurus silesiacus,* Arthaber, p. 473.
1928 *Cymatosaurus* (?) *gracilis,* Schmidt, p. 394, Fig. 1107.
1928 *Cymatosaurus latifrons,* Schmidt, p. 394, Fig. 1108.
1928 *Cymatosaurus silesiacus,* Schmidt, p. 394, Figs. 1106a–b.
1934 *Cymatosaurus gracilis,* Kuhn, p. 43.
1934 "*Nothosaurus*" *latifrons,* Kuhn, p. 34.
1934 *Cymatosaurus silesiacus,* Kuhn, p. 42.
1935 *Cymatosaurus silesiacus,* Edinger, Fig. 9c.
1944 *Cymatosaurus gracilis,* E.v. Huene, pp. 198 *f.*, 208.
1944 *Cymatosaurus latifrons,* E.v. Huene, pp. 198 *f.*, 207 *f.*
1944 *Cymatosaurus silesiacus,* E.v. Huene, pp. 198 *f.*, 208.
1964 *Cymatosaurus gracilis,* Kuhn, p. 12.

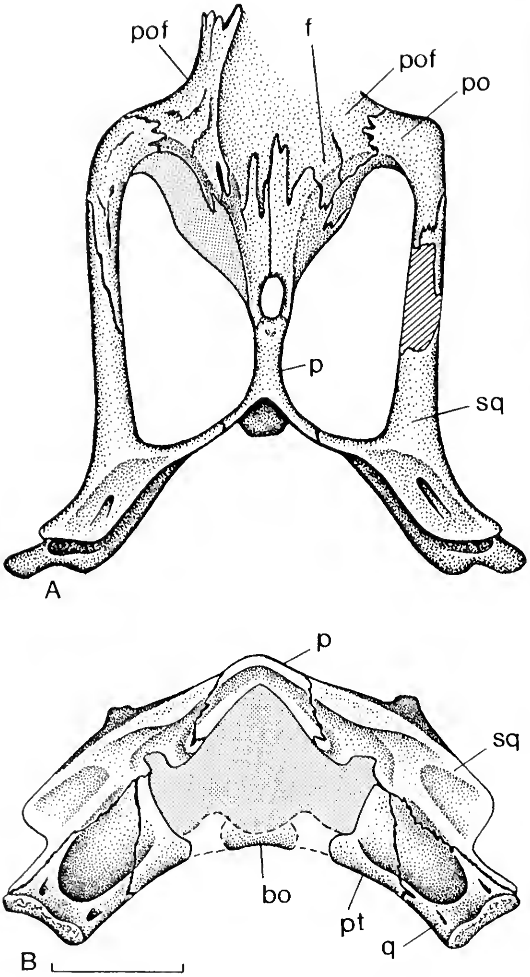

FIG. 3. A fragmentary skull (BGR S 44/3) from the lower Muschelkalk of Gogolin, Upper Silesia, referred to *Cymatosaurus fridericianus* v. Fritsch, 1894. **A,** Dorsal view; **B,** occipital view. Scale bar = 20 mm. Abbreviations: bo, basioccipital; f, frontal; p, parietal; po, postorbital; pof, postfrontal; pt, pterygoid; q, quadrate; sq, squamosal.

1964 *Nothosaurus* (?*Cymatosaurus*) *latifrons,* Kuhn, p. 8.

1964 *Cymatosaurus silesiacus,* Kuhn, p. 13.

NEOTYPE—The skull described by Gürich (1884) and figured by Frech (1903, Figs. 2a–c) can no longer be located in public repositories. Schrammen's (1899) second specimen of *Cymatosaurus "gracilis"* (SMNS 10109; Figs. 5–6) is the only complete skull of *Cymatosaurus latifrons* available today and is here designated the neotype.

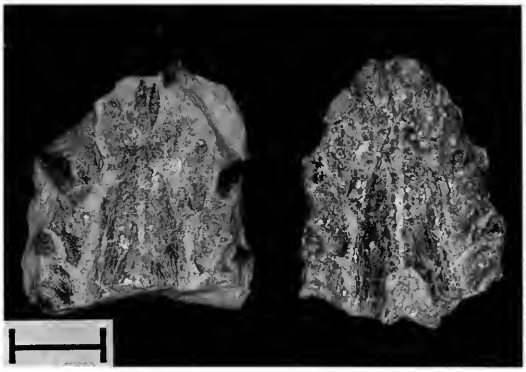

FIG. 4. A snout fragment of *Cymatosaurus* cf. *C. fridericianus* (SMNS 7209) from the lower Muschelkalk of Freudstadt. Scale bar = 20 mm.

LOCUS TYPICUS—Lower Muschelkalk (Gogolin beds, mu_1), Gogolin, Upper Silesia (Poland); for the neotype: lower Muschelkalk (Gogolin beds, mu_1), Krappitz (Krapkowice), Upper Silesia (Poland).

DIAGNOSIS—A species of *Cymatosaurus* of intermediate size[1] (tip of snout to back end of partial skull table up to 150 mm); single maxillary tooth preceding paired maxillary fangs; pre- and postfrontal may or may not be in contact at dorsal margin of orbit; frontal may closely approach but does not enter anteromedial margin of upper temporal fossa.

DISTRIBUTION—Lower Muschelkalk (lower Anisian, lower Middle Triassic), central Europe.

REFERRED SPECIMENS—BGR S 44/3 (complete but poorly preserved skull, lower Muschelkalk [lower Gogolin beds], Sacrau near Gogolin; SMNS 10977 (incomplete skull, uppermost Buntsandstein [Coelestinschichten, uppermost Röt], Jenzig near Jena [Rieppel, 1994b, Fig. 11]).

COMMENTS—The original (type) material of *Cymatosaurus latifrons* (Gürich, 1884) can no longer be located today. Frech (1903) figured the specimen after additional preparation, but unfortunately published the photograph with retouched suture lines. Following Frech's (1903) interpretation, the nasals remain excluded from the posterior margin of the external nares, as in *Cymatosaurus frider-*

[1] A small and as yet undescribed species of *Cymatosaurus* from the lower Muschelkalk of Thuringia differs from other species of its genus by relatively long and narrow upper temporal fenestrae and the presence of a sagittal crest. The species will be described elsewhere in collaboration with R. Werneburg, Natural History Museum Schleusingen.

TABLE 1. Skull proportions in *Cymatosaurus, Germanosaurus,* and *Nothosaurus.*

	Cymatosaurus	*Germanosaurus*	*Nothosaurus*
snout - orbit / snout - external naris	1.9 - 2.0	1.8	1.6 - 2.0
snout - temporal fossa / snout - external naris	2.7 - 3.0	2.86	2.3 - 3.4
long. Ø temporal fossa / long. Ø orbit	**1.3 - 2.0**	**1.87**	2.1 - 3.9
snout - internal nares / snout - external nares	**1.2 - 1.43**	**1.33**	1.04 - 1.16

icianus and in Schrammen's (1899) "second" specimen (see below for details of Schrammen's original material) of *Cymatosaurus gracilis.* The frontals appear to closely approach the anteromedial margin of the upper temporal fossa, but they remain excluded from them. Prefrontal and postfrontal are in contact at the dorsal margin of the upper temporal fossa, as in *Cymatosaurus fridericianus,* in Schrammen's (1899) "first" specimen of *Cymatosaurus silesiacus,* and in Schrammen's (1899) "second" specimen of *Cymatosaurus gracilis*; in Schrammen's (1899) "first" specimen of *Cymatosaurus gracilis,* prefrontal and postfrontal remain separated at the dorsal margin of the orbit. In the (lost) holotype of *Cymatosaurus latifrons,* the width of the dorsal bridge between the orbits (12 mm) is 1.7 times the width of the dorsal bridge between the external nares (7 mm), and the distance from the external naris to the orbit is approximately 2.8 times the width of the postorbital arch. With these values, the (lost) holotype of *Cymatosaurus latifrons* combines values otherwise typical for *Cymatosaurus gracilis* and *Cymatosaurus silesiacus.*

Schrammen (1899) described *Cymatosaurus gracilis* on the basis of two specimens, one an incomplete skull exposed in dorsal view (Schrammen's [1899, Pl. 23, Fig. 2] first specimen from Sacrau near Gogolin, kept in a private collection [Grundey]), the other a complete skull exposed in ventral view (Schrammen's [1899, Pl. 23, Fig. 3] second specimen from Krappitz [Krapkowice], kept in his own collection). The first specimen cannot be located today; the second specimen (SMNS 10109) has been prepared from the dorsal side for this study. As emphasized by Schrammen (1899), *Cymatosaurus gracilis* differs from *Cymatosaurus silesiacus* mainly in absolute size. Schrammen's (1899) "second" specimen of *Cymatosaurus gracilis* measures 98 mm from the tip of the snout to the back end of the parietal skull table; his "first" specimen of *Cymatosaurus silesiacus* measures approximately 145 mm (an undescribed and rather poorly preserved specimen [BGR S 44/3] has a corresponding skull length of 125 mm). Apart from absolute size, *Cymatosaurus gracilis* differs from *Cymatosaurus silesiacus* by relatively larger orbits. In *Cymatosaurus gracilis* the distance from the external naris to the orbit equals less than 2.5 times the width of the postorbital arch, whereas in *Cymatosaurus silesiacus* it exceeds 2.5 times the width of the postorbital arch. In *Cymatosaurus gracilis,* the width of the dorsal bridge between the orbits is less than twice the width of the dorsal bridge between the nares; in *Cymatosaurus silesiacus,* it exceeds twice the width of the bridge between the external nares. Because the orbit grows with negative allometry in sauropterygians, relatively large orbits in relatively small skulls are not diagnostic of a separate species, and *Cymatosaurus gracilis* is considered to be represented by juvenile individuals.

Schrammen (1899) described *Cymatosaurus silesiacus* on the basis of two skulls. His first specimen, from Sacrau near Gogolin (Schrammen, 1899, Pls. 21–22), was kept in a private collection (Grundey) and cannot be located in public repositories today. The second specimen, a fragmentary skull associated with postcranial remains from Krappitz [Krapkowice], was kept in Schrammen's own collection and likewise cannot be located in public repositories today. The skull of the "first" specimen described by Schrammen (1899) was fairly well preserved, and although the dermal bones were all finely broken, Schrammen (1899) asserted that sutures could be identified with great confidence. As described by Schrammen (1899), *Cymatosaurus silesiacus* shows an interesting combination of features such as nasals entering the posterior margin of the external naris, prefrontal and postfrontal in contact along the dorsal margin of the orbit, and exclusion of the frontal from the anteromedial margin of the upper temporal fossa. *Cymatosaurus silesiacus* shares with *Cymatosaurus gracilis* (but not with *Cymatosaurus fridericianus*) a single maxillary tooth preceding the paired maxillary fangs. Comparison to the outgroup (Nothosauridae: Rieppel, 1994b) shows

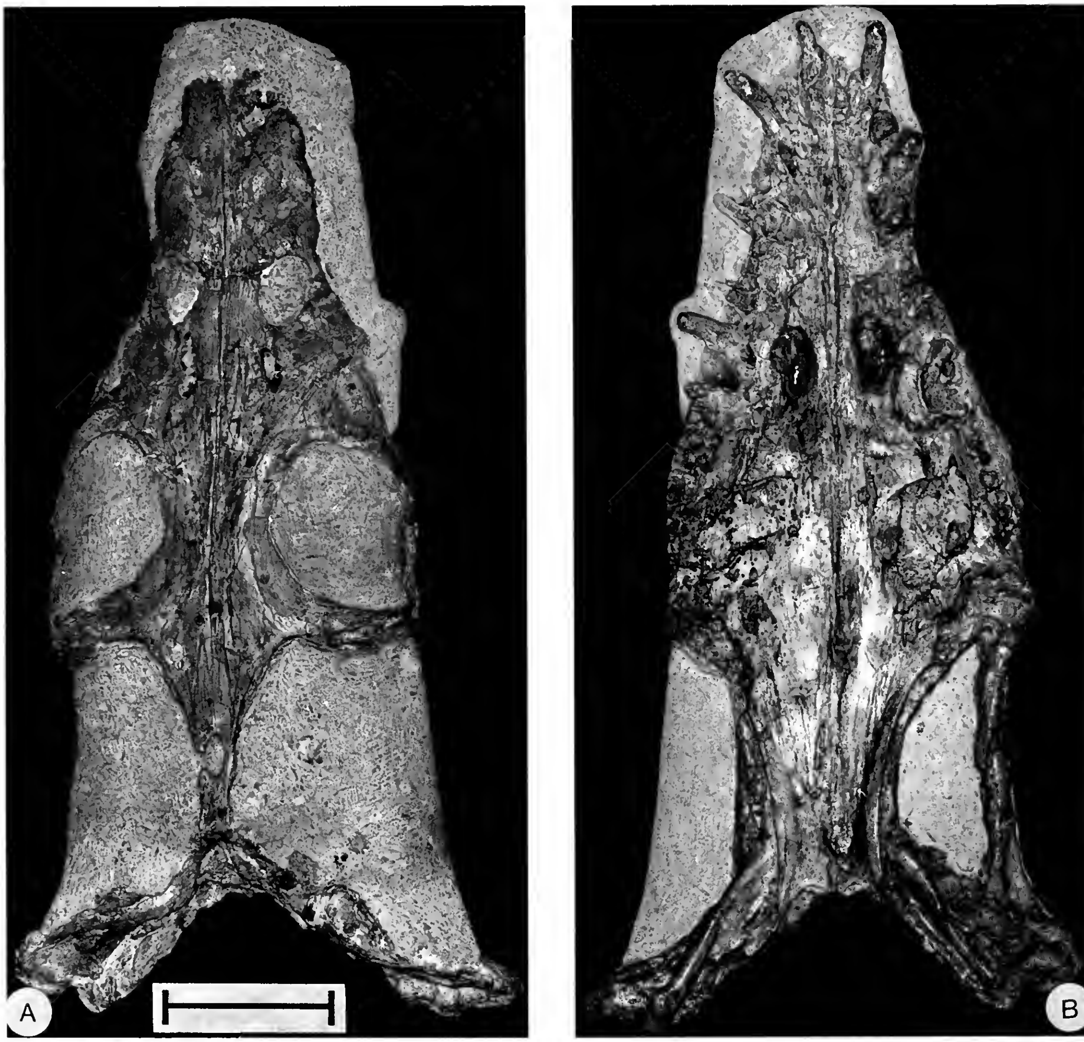

FIG. 5. The skull of the neotype of *Cymatosaurus latifrons* (Gürich, 1884) (SMNS 10109), from the lower Muschelkalk of Krapkowice, Upper Silesia. **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm.

this to be a derived character, diagnostic of a separate species for which *Cymatosaurus latifrons* Gürich, 1884, takes priority.

MORPHOLOGICAL DESCRIPTION—The description of the skull will primarily be based on the neotype (SMNS 10109; Figs. 5–6); reference will be made to the referred specimen SMNS 10977 (Rieppel, 1994b, Fig. 11) where necessary. In contrast to SMNS 10977, the neotype is strongly compressed dorsoventrally, and its small size indicates a juvenile status. Reference of both skulls to *Cymatosaurus* is corroborated by the paired frontals and the incompletely fused parietals, the contact of prefrontal and postfrontal along the dorsal margin of the orbit, the restriction of the maxillary tooth row to a level in front of the anterior margin of the upper temporal fossa, and the location of the pineal foramen at the center of the parietal skull table.

Total length of the skull of SMNS 10109 (as preserved) is 104 mm; the distance from the tip of the snout to the posterior end of the parietal skull table measures 98 mm. The rostrum is narrow and elongated. Its relative length does not differ in *C. latifrons* and in *C. fridericianus*: dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris

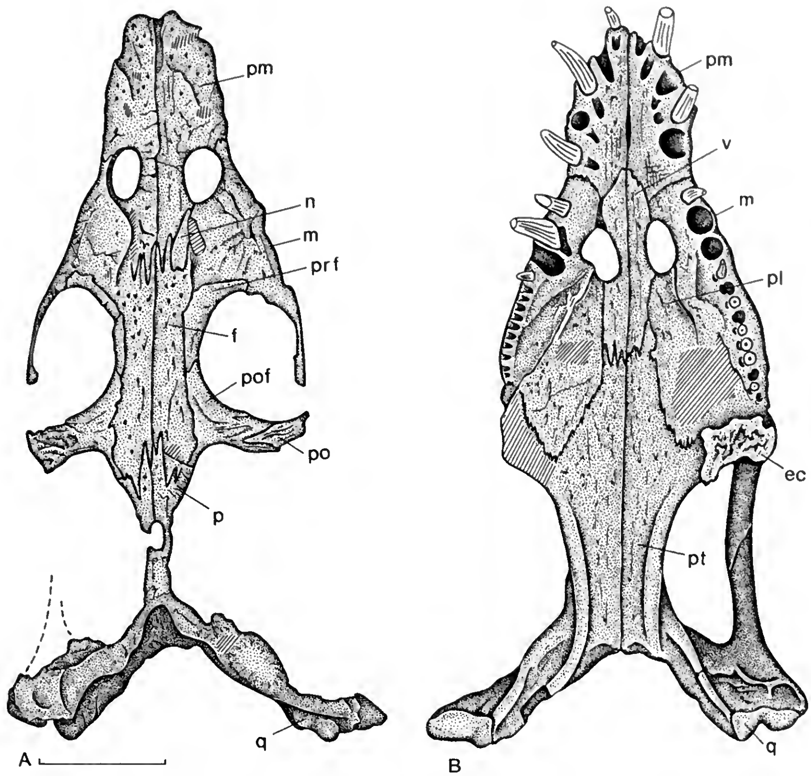

FIG. 6. The skull of the neotype of *Cymatosaurus latifrons* (Gürich, 1884) (SMNS 10109) from the lower Muschelkalk of Krapkowice, Upper Silesia. **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm. Abbreviations: ec, ectopterygoid; f, frontal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; v, vomer.

yields values of 1.87 for the holotype of *C. fridericianus* and 2.0 for the neotype of *C. latifrons.* Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fossa by the distance from the tip of the snout to the anterior margin of the external naris yields values of 2.68 for the holotype of *C. fridericianus* and 3.0 and for the neotype of *C. latifrons.* The somewhat larger value in the latter species may be due to relatively larger orbits in this juvenile specimen. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the maximum width of the premaxillary rostrum yields values of 1.4 for the holotype of *C. fridericianus* and 1.2 for the neotype of *C. latifrons.* Dividing the dorsal bridge between the orbits by the dorsal bridge between the external nares yields values of 2.4 for the holotype of *C. fridericianus* and 1.6 for the neotype of *C. latifrons.* This indicates a relatively narrower dorsal bridge between the orbits in the latter species, again a consequence of relatively large orbits in this juvenile specimen. Schrammen's (1899) first specimen of *C. "gracilis"* would show a corresponding ratio of 1.5, whereas in the larger *C. "silesiacus"* (Schrammen, 1899; first specimen) the ratio is 2.9. The original holotype of *Cymatosaurus latifrons* Gürich, 1884, again a relatively small skull (tip of snout to posterior end of parietal skull table approximately 100 mm), shows a corresponding value of 1.7. The relatively large size of the orbits is also borne out by the quotient which results from division of the distance between the external naris and the orbit by the distance between the orbit and the upper temporal arch. The quotient is 2.8 for the holotype of *C. fridericianus* and 2.3 for the neotype of *C. latifrons.* Schrammen's (1899) first specimen of *C. "gracilis"* would show a corresponding ratio of 1.7, whereas in the larger *C. "silesiacus"* (Schrammen, 1899; first specimen) the ratio is 2.6.

The paired premaxillae meet the maxillae at the anterolateral corner of the external naris, and they form a broad and interdigitating contact with the

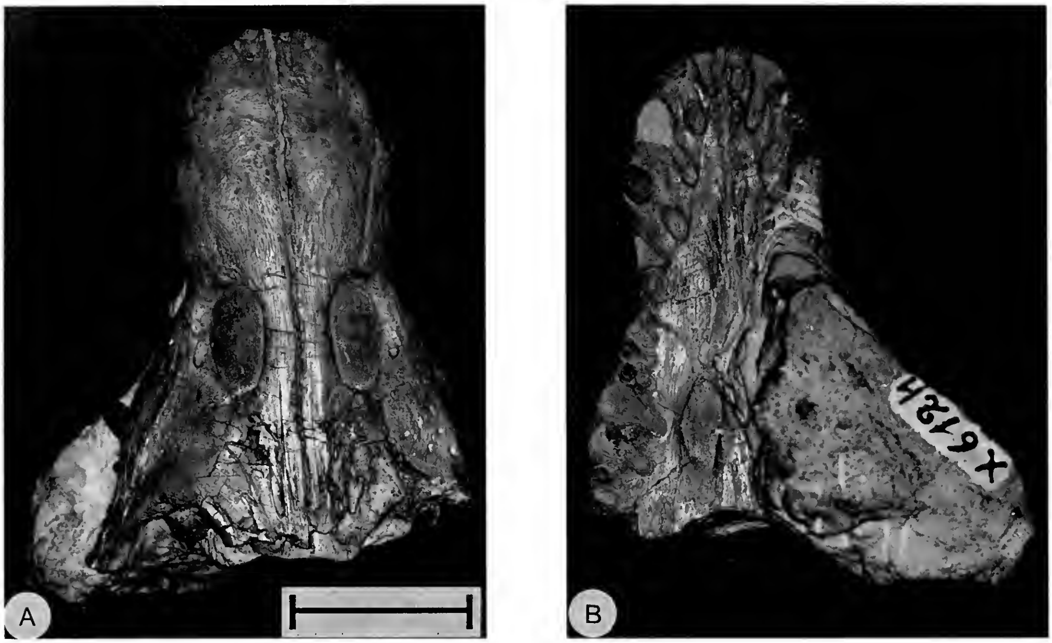

FIG. 7. The holotype of *Cymatosaurus erythreus* E.v. Huene, 1894 (BGR 612), from the upper Buntsandstein of Rüdersdorf near Berlin, **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm.

paired frontals between the nasals, at a level between the external nares and the orbits. The external nares are relatively broad and rounded. The left nasal cannot be identified in SMNS 10109 because of excessive original preparation of the internal naris, but the reduced right nasal can be seen to be excluded from the posterior margin of the external naris, unlike in Schrammen's (1899, Pl. 23, Fig. 2) "first specimen" of *C.* "*gracilis*"; in that respect, the latter specimen resembles the holotype of *C. silesiacus* (Schrammen, 1899, Pl. 21). Laterally, the nasal remains separated from the prefrontal by a broad contact between an anterolateral process of the frontal and the maxilla. Exclusion of the reduced nasals from the external naris and separation of the nasal from the prefrontal by a frontal–maxillary contact are also observed in SMNS 10977. The prefrontal appears as a rather slender element in dorsal view, lining the anterodorsal margin of the orbit and establishing a contact with the postfrontal that excludes the frontal from the orbit (unlike in Schrammen's [1899, Pl. 23, Fig. 2] first specimen, but as in the holotype of *C. silesiacus,* and as in SMNS 10977). The frontal forms a distinct posterolateral process that remains narrowly excluded from the anteromedial margin of the upper temporal fossa (as in Schrammen's "first specimen," the posterolateral process of the frontal approaches the upper temporal fossa less closely in SMNS 10977). The postfrontal is a relatively broad element that defines the posterodorsal margin of the orbit as well as the anteromedial margin of the upper temporal fossa. It meets the postorbital in a deeply interdigitating suture within the postorbital arch. The lateral (ventral) part of the postfrontal, and its relation to the jugal and to the upper temporal arch, are not preserved on either side of the skull. SMNS 10977 shows the postorbital to meet the squamosal in a broadly overlapping suture within the upper temporal arch. The jugal is a curved element without posterior process that defines the posteroventral corner of the orbit.

The interdigitating frontoparietal suture is located between the anterior parts of the upper temporal fenestrae. To judge from the shape of the lateral margin of the parietal, the anterior, medial, and posterior margins of the relatively broad upper temporal fossa were more or less evenly curved. The pineal foramen is located at the center of the parietal skull table. In front of the pineal foramen, a distinct suture separates the paired parietals (the parietals are fully fused in SMNS 10977). Behind the pineal foramen, the parietal is distinctly constricted but not developed into a sagittal crest. No trace of a medial longitudinal suture

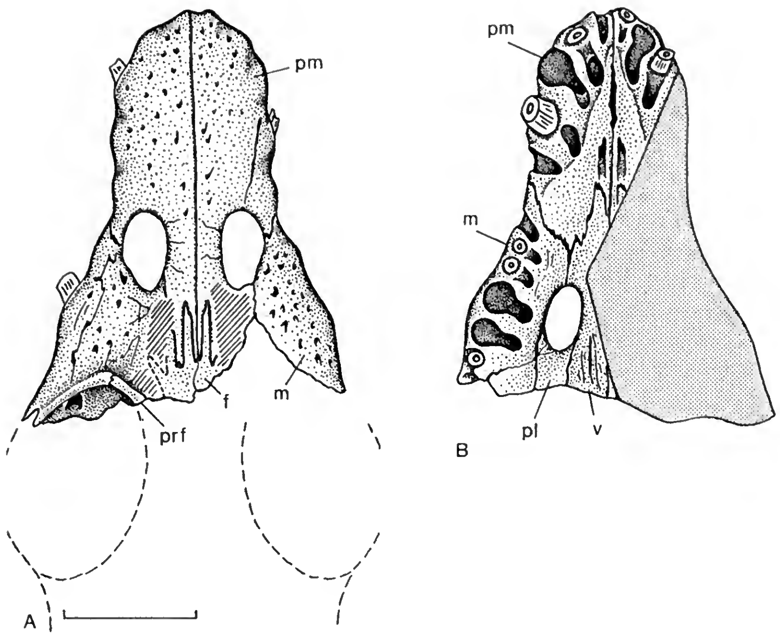

FIG. 8. The holotype of *Cymatosaurus erythreus* E.v. Huene, 1894 (BGR 612), from the upper Buntsandstein of Rüdersdorf near Berlin. **A,** Dorsal view; **B,** ventral view. Scale bar = 20 mm. Abbreviations; f, frontal; m, maxilla; pl, palatine; pm, premaxilla; prf, prefrontal; v, vomer.

can be identified in the constricted posterior part of the parietal skull table.

Preservation of the occiput is incomplete in SMNS 10109. As preserved, the skull contours indicate a deeply concave occiput and a limited occipital exposure of the parietal. Poor preservation makes it impossible to trace the suture between the parietal and squamosal. All posterior braincase elements (supraoccipital, exoccipitals, opisthotic, and basioccipital [occipital condyle]) are missing. This indicates a loose connection between the braincase and the dermatocranium, which might be attributed to the juvenile status of the specimen. However, all posterior braincase elements are also missing in the larger specimen SMNS 10977, as indeed in every other specimen of *Cymatosaurus* available today. It is for this reason that a tight association of the braincase with the dermatocranium in the formation of a closed, plate-like occiput (as seen in *Simosaurus* and *Nothosaurus*) is believed to be absent in *Cymatosaurus* (characters 31 and 32 of the cladistic analysis, discussed below). The suspensorium appears to be distinctly flaring in SMNS 10109, carrying the mandibular articulation to a position well lateral of the posterior corner of the upper temporal fossa. This is, however, an artifact of dorsoventral crushing of the skull. In the three-dimensionally preserved specimen SMNS 10977, the suspensorium is more vertically oriented, and the mandibular articulation is positioned below the posterior end of the upper temporal fossa, as is typical for the genus in general.

The ventral view of the skull shows five premaxillary tooth positions and a single maxillary tooth preceding the paired maxillary fangs (three maxillary teeth precede the paired maxillary fangs in *C. fridericianus*). Behind the maxillary fangs, 10–11 tooth positions can be counted, bringing the total number of maxillary teeth up to 13–14. The same tooth count is obtained in SMNS 10977. Posteriorly, the maxillary tooth row does not extend beyond the level of the posterior margin of the orbit. The internal nares are relatively shorter than in *C. fridericianus* (division of the longitudinal diameter by the transverse diameter yields a ratio of 1.6 for SMNS 10109), but as in the latter species, and unlike *Nothosaurus,* the internal naris is positioned somewhat further back relative to the external naris (Table 1).

A narrow fontanelle ("foramen incisivum") separates the premaxillae in ventral view. The paired vomers meet the maxillae at the anterior margin of the internal nares, thus excluding the premaxillae from the latter. Posteriorly, the vomers meet the pterygoids in an interdigitating suture. The posterior margin of the internal naris is defined by the palatine. The exact contours of the ectopterygoid cannot be identified, but the presence of a well-developed (ecto-)pterygoid flange is distinct on the left side of the skull. Posteriorly, the pterygoid shows well-developed lateral and medial ventral flanges for the origin of the pterygoideus musculature.

Cymatosaurus multidentatus (F.v. Huene, 1958)

1958 *Anarosaurus multidentatus,* F.v. Huene, pp. 382–384.
1995c *Cymatosaurus multidentatus,* Rieppel, p. 288.

HOLOTYPE—Incomplete lower jaw (Mbg 4791).

LOCUS TYPICUS—Lowermost lower Anisian (6 m above the base), Krabachmasse, Trittwangkopf, NNW Stuttgarter Hütte, Lechtaler Alpen (Arlberg), Austria.

DIAGNOSIS—A very incompletely known species of *Cymatosaurus* of small size, characterized by a distinctly heterodont dentition.

REFERRED SPECIMENS—Mbg 4792 (isolated tooth [Huene, 1958, Fig. 2], fragmentary vertebra); Mbg 4793 (isolated tooth [Huene, 1958, Fig. 3]. ?metatarsal [Huene, 1958, Fig. 6]); Mbg 4794 (vertebral centrum [Huene, 1958, Fig. 24); Mbg 4795 (fragmentary vertebral centrum [Huene, 1958, Fig. 5]).

COMMENTS—This species was redescribed by Rieppel (1995c).

Cymatosaurus sp. ("*C. erythreus*" E.v. Huene, 1944)

Synonymy for this material:

1994 *Cymatosaurus erythreus,* E.v. Huene, pp. 193 *ff.,* Figs. 1a–c.
1964 *Cymatosaurus erythreus,* Kuhn, p. 13.
1995c *Cymatosaurus erythreus,* Rieppel, p. 295, Figs. 7, 8C.

HOLOTYPE—Snout fragment (BRG 612; Figs. 7, 8).

LOCUS TYPICUS—Upper Buntsandstein (so_2, Röt), Rüdersdorf near Berlin.

REFERRED SPECIMEN—An isolated parietal (Fig. 9; BGR 613; original of E.v. Huene, 1994, p. 200, Fig. 2 in her paper) from the same locality and horizon as the holotype.

COMMENTS—This species was described by E.v. Huene (1944) on the basis of an incomplete skull that represents the earliest occurrence of the genus *Cymatosaurus* in the Germanic Triassic. The fragment (Figs. 7, 8) comprises most of the preorbital skull and has a total length of 58.4 mm (as preserved). The distance from the tip of the snout to the anterior margin of the external naris is 29 (28) mm, to the anterior margin of the orbit 54 mm. The longitudinal diameter of the external naris is 12.2 mm, and the bridge between the external naris and the orbit is 13.5 mm wide. The width of the snout at the level of the anterior margins of the external nares is 23.5 mm; the total width of the premaxillary rostrum (at the fourth tooth position) is 25.7 mm. The longitudinal diameter of the internal naris is 9.5 mm.

The rostrum is of similar relative length as in the genotypical species, *Cymatosaurus fridericianus* Fritsch (1894), or, indeed, as in other species of *Cymatosaurus.* Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in a ratio of 1.89 for *Cymatosaurus erythreus,* compared to 1.87 for *Cymatosaurus fridericianus.*

The rostrum is formed by the premaxillae. Broad posterior (nasal) processes of the premaxillae separate the external nares from one another and meet the frontals in a deeply interdigitating suture at a level between the external nares and the orbits. The preserved anterior ends of the frontals show these elements to be paired, as is characteristic of the genus *Cymatosaurus.*

Damage to the bone surface has rendered the accurate delineation of the nasals impossible. However, the nasal extends anteriorly along the medial margin of the external naris in those stem-group sauropterygians that do not show reduction of these elements. No participation of the nasals can be identified in the medial margins of the external nares in *Cymatosaurus erythreus,* indicating reduction of these bones. Likewise, the left external naris indicates the exclusion of the nasal from its posterior margin, another feature diagnostic for (some) *Cymatosaurus.*

The prefrontal is exposed at the anterodorsal margin of the left orbit. A lacrimal is lacking

FIG. 9. An isolated parietal referred to *Cymatosaurus erythreus* E.v. Huene, 1894 (BGR 613), from the upper Buntsandstein of Rüdersdorf near Berlin. Scale bar = 20 mm.

(contra E.v. Huene, 1944, p. 195), and the lacrimal duct is enclosed entirely within the maxilla, as is also observed in *Nothosaurus*.

The ventral aspect reveals relatively short and broad internal nares, a feature shared with other species of *Cymatosaurus* but a contrast to the relatively narrow and elongated internal nares observed in *Nothosaurus* (except *N. marchicus*). The posterior margin of the internal naris is defined by the palatine and its medial margin by the (paired) vomer. Vomer and maxilla meet in a broad contact at the anterior margin of the internal naris, thus excluding the premaxilla from the latter. Between the premaxillae and in front of the vomers, a fontanelle persists, a feature shared with *Cymatosaurus, Pistosaurus* (Fritsch, 1894), and *Nothosaurus* (Rieppel & Wild, 1996). The right premaxilla carries five tooth positions; the size of the alveoli indicates that the third and fourth teeth were the largest. Three small maxillary teeth precede the paired maxillary fangs. The replacement pits, located posteromedial to the functional tooth positions, are more distinctly elongated and drop-shaped than in *Nothosaurus*, and most of them are confluent with the alveoli of the functional teeth.

The skull fragment described by E.v. Huene (1944) as *Cymatosaurus erythreus* is unquestionably a representative of that genus, as is indicated by a number of characters, most notably the exclusion of the (reduced) nasals from the external naris and the paired condition of the frontals. The specimen is too incomplete, however, to be diagnostic for a separate species. Within the genus, it shares with *Cymatosaurus fridericianus* three small maxillary teeth preceding the maxillary fangs, but this is a plesiomorphic trait in comparison to the outgroup (Nothosauridae). Therefore, *Cymatosaurus erythreus* E.v. Huene, 1944, is here considered a nomen dubium.

Nothosauridae Baur, 1889

DEFINITION—A monophyletic taxon including the genera *Germanosaurus* Nopcsa, 1928a, *Nothosaurus* Münster, 1834, and *Lariosaurus* Curioni, 1847 (*Ceresiosaurus* Peyer, 1931, and *Silvestrosaurus* Kuhn-Schnyder, 1990, are here considered junior synonyms of *Lariosaurus*: Rieppel, 1993, and in prep.).

DIAGNOSIS—Small to large eosauropterygians with a strongly depressed skull; snout constricted; dorsal exposure of prefrontal reduced; jugal (usually) excluded from posterior margin of orbit; premaxillary and anterior dentary fangs present.

DISTRIBUTION—Lower to Upper Triassic, Europe and Israel.

COMMENTS—Within the Nothosauridae, *Germanosaurus* is the sister-taxon of a monophyletic clade (Nothosaurinae: Nopcsa, 1923, 1928a,b) including the genera *Nothosaurus* and *Lariosaurus*. Diagnostic characters of the Nothosaurinae are frontals fused, parietal skull table strongly constricted, maxillary fangs present, occipital crest present, supraoccipital horizontally oriented and fused with parietal, occipital crest present, mandibular symphysis strongly elongated and fortified (not known for *Germanosaurus*), unconstricted vertebral centra (not known for *Germanosaurus*), and no distal expansion of sacral ribs (not known for *Germanosaurus*).

Germanosaurus Nopcsa, 1928

1903 *Eurysaurus,* Frech, p. 15.
1924 *Eurysaurus,* Arthaber, p. 476.

1928a *Germanosaurus,* Nopcsa, pp. 21, 44.
1928b *Germanosaurus,* Nopcsa, p. 173.
1944 *Cymatosaurus* (*Germanosaurus*) (partim), E.v. Huene, p. 208.

TYPE SPECIES—*Germanosaurus latissimus* Gürich, 1891, from the lower Muschelkalk, lower Middle Triassic, Sacrau, Upper Silesia.

DEFINITION—A monophyletic taxon including the species *schafferi.*

DIAGNOSIS—A large eosauropterygian with a constricted snout and a relatively short and broad rostrum. Posterolateral process of paired frontals closely approaches upper temporal fossa; parietals paired.

COMMENTS—Of the two species described in the genus, *Germanosaurus latissimus* (Gürich, 1891) and *Germanosaurus schafferi* (Arthaber, 1924), only the latter is represented by original material available today.

Germanosaurus sp. ("*G. latissimus*" [Gürich, 1891])

Synonymy for this material:

1891 *Nothosaurus latissimus,* Gürich, p. 968, Figs. a–b.
1893 *Nothosaurus latissimus,* Koken, p. 368 *ff.,* Figs. 6–11.
1899 *Cymatosaurus* (*Nothosaurus*) *latissimus,* Schrammen, p. 388 *f.*
1903 *Nothosaurus* (*Eurysaurus*) *latissimus,* Frech, p. 15, Fig. 1.
1914 *Nothosaurus* (*Eurysaurus*) *latissimus,* Schröder, p. 78.
1914 *Eurysaurus latissimus,* Schröder, p. 82 *ff.,* Fig. 22.
1924 *Eurysaurus latissimus,* Arthaber, p. 476 *f.*
1928 *Eurysaurus latissimus,* Schmidt, p. 395, Fig. 1110.
1934 *Germanosaurus latissimus,* Kuhn, p. 41.
1944 *Cymatosaurus latissimus,* E.v. Huene, p. 199.
1944 *Cymatosaurus* (*germanosaurus*) *latissimus,* E.v. Huene, p. 208.
1964 *Cymatosaurus latissimus,* Kuhn, p. 13.

HOLOTYPE—The skull described by Gürich (1891) and figured by Koken (1893, Fig. 10) and Frech (1903, Fig. 1) can no longer be located in public repositories.

LOCUS TYPICUS—Lower Muschelkalk (Gogolin beds, mu_1), Sacrau near Gogolin, Upper Silesia (Poland).

COMMENTS—The taxonomic status of "*Cymatosaurus*" *latissimus* (Gürich, 1891) can no longer be critically evaluated because the original (type) material has been lost. The situation is aggravated by the fact that Gürich (1891, figure on p. 968) included only a very schematic figure in his original description of the species. The skull was preserved in two parts and estimated by Gürich (1891) to be approximately 270 mm long. With this size, the specimen is distinctly larger than any specimen of *Cymatosaurus* but closely approaches the holotype of *Germanosaurus schafferi* (Arthaber, 1924). Koken (1893, Fig. 11) indicates four maxillary teeth preceding the paired maxillary fangs, a character that separates "*Cymatosaurus*" *latissimus* from the known species of *Cymatosaurus.* In other respects, however, "*Cymatosaurus*" *latissimus* resembles *Germanosaurus schafferi,* with which it shares the reduced nasal bones that enter the posterior margin of the external nares, the paired frontals, the restricted dorsal exposure of the prefrontals (broadly exposed in *Cymatosaurus*), which do not contact the postfrontal along the dorsal margin of the orbit, and a jugal bone that extends alongside the postorbital into the upper temporal arch (the jugal does not extend into the upper temporal arch in *Cymatosaurus* as shown by the specimen SMNS 10977). Whether the jugal does, indeed, broadly enter the ventral margin of the orbit in "*Cymatosaurus*" *latissimus* (Koken, 1893, Fig. 10), or whether is was excluded therefrom, can no longer be assessed. In view of its large size and the characters outlined above, "*Cymatosaurus*" *latissimus* is here referred to the genus *Germanosaurus. Germanosaurus latissimus* (Gürich, 1891) is here treated as a nomen dubium rather than as a senior synonym of *Germanosaurus schafferi* (Arthaber, 1924), because loss of the holotype (and only known specimen) prevents critical comparison with the latter species.

→

FIG. 10. The skull of the holotype of *Germanosaurus schafferi* (Arthaber, 1924) (NHMW, uncatalogued), from the lower Muschelkalk of Gogolin, Upper Silesia, in dorsal view. Scale bar = 50 mm. (Courtesy of Dr. G. Höck, Natural History Museum, Vienna.)

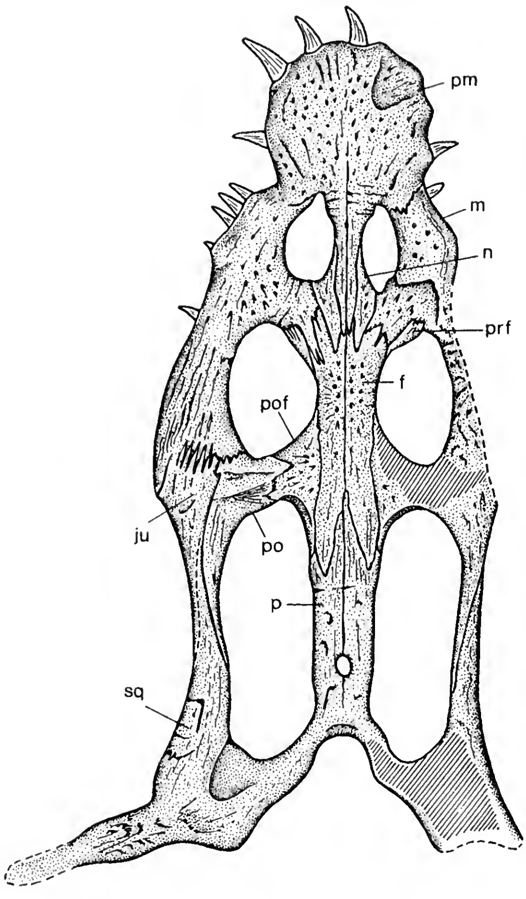

FIG. 11. The skull of the holotype of *Germanosaurus schafferi* (Arthaber, 1924) (NHMW, uncatalogued), from the lower Muschelkalk of Gogolin, Upper Silesia, in dorsal view. Scale bar = 50 mm. Abbreviations: f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; sq, squamosal.

Germanosaurus schafferi (Arthaber, 1924)

1924 *Eurysaurus schafferi,* Arthaber, p. 1476 *ff.,* Figs. 11a–b.
1928 *Eurysaurus schafferi,* Schmidt, p. 395, Fig. 1111.
1934 *Germanosaurus schafferi,* Kuhn, p. 42.
1944 *Cymatosaurus* (*Germanosaurus*) *schafferi,* E.v. Huene, p. 208 *f.*
1964 *Cymatosaurus schafferi,* Kuhn, p. 12.

HOLOTYPE—Skull (NHMW, uncatalogued; Figs. 10, 11).

LOCUS TYPICUS—Lower Muschelkalk (Gogolin beds, mu_1), Gogolin, Upper Silesia (Poland).

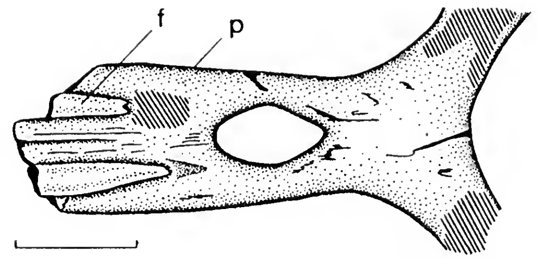

FIG. 12. An isolated parietal referred to *Germanosaurus schafferi* (Arthaber, 1924) (BGR, uncatalogued), from the lower Muschelkalk of Gogolin, Upper Silesia. Scale bar = 50 mm. Abbreviations: f, frontal; p, parietal.

DIAGNOSIS—Same as for genus, of which this is the only species represented by original material today.

DISTRIBUTION—Lower Muschelkalk (lower Anisian, lower Middle Triassic), central Europe.

REFERRED SPECIMENS—Isolated parietal (Fig. 12) from the lower Muschelkalk (Gogolin beds, mu_1), Gogolin, Upper Silesia (BGR, uncatalogued; Rieppel, 1994a, Fig. 40).

MORPHOLOGICAL DESCRIPTION—*Germanosaurus schafferi* is known from a single skull prepared in dorsal view (Fig. 11). The distance from the tip of the snout to the back end of the parietal skull table measures 244 mm, which is distinctly longer than in the skulls referred to the genus *Cymatosaurus* but approaches the size of "*Cymatosaurus*" *latissimus* (see above). The rostrum is relatively broader than in skulls referred to the genus *Cymatosaurus,* with the consequence that the rostral constriction is more pronounced in *Germanosaurus.* Dividing the distance from the tip of the snout to the anterior margin of the external

TABLE 2. Data matrix for the cladistic analysis of all *Cymatosaurus* species ever described. Character definitions are given in the Appendix.

	1	1	2	3	4	5
1	erythreus	1	?	?	?	?
2	fridericianus	1	1	1	0	0
3	gracilis I	0	0	0	?	1
4	gracilis II	1	1	0	1	1
5	latifrons	1	1	0	?	0
6	latissimus	0	0	0	?	?
7	silesiacus I	0	1	0	1	0
8	SMNS 10977	0	1	0	?	?
9	BRG uncat	?	1	1	?	?
10	All-0-Anc	0	0	0	0	0

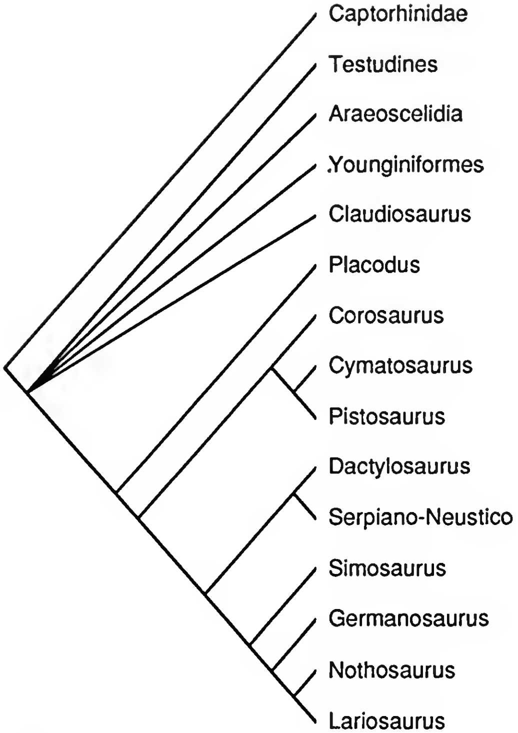

FIG. 13. Strict consensus tree (2 MPTs, TL = 283, CI = 0.675, RI = 0.702) for a monophyletic Sauropterygia rooted on Captorhinidae, Araeoscelidia, Younginiformes, *Claudiosaurus,* and Testudines. For further discussion see text.

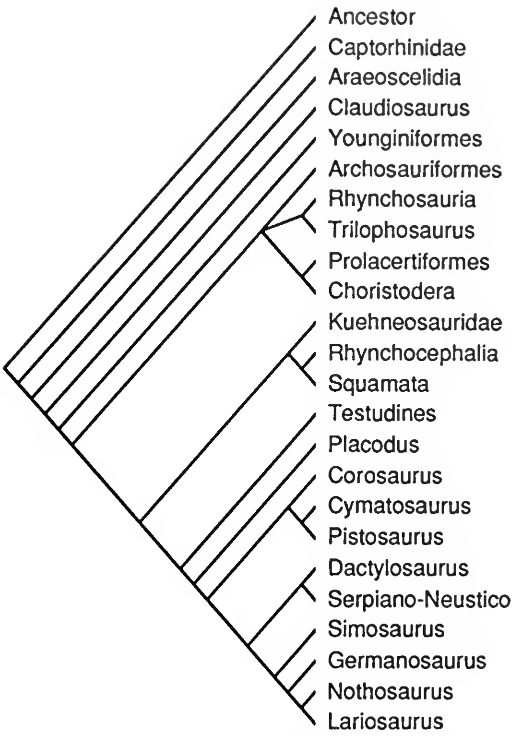

FIG. 14. Strict consensus tree (2 MPTs, TL = 452, CI = 0.648, RI = 0.711) for 23 ingroup taxa rooted on an all-0 ancestor. For further discussion see text.

naris by the maximum width of the premaxillary rostrum yields values of 0.94 (left side) and 1.03 (right side) for the holotype of *Germanosaurus schafferi,* 1.4 for the holotype of *C. fridericianus,* and 1.2 for the neotype of *C. latifrons.* Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris yields a value of approximately 1.8 for the holotype of *Germanosaurus schafferi,* 1.9 for the holotype of *C. fridericianus,* and 2.0 for the neotype of *C. latifrons.* Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fossa by the distance from the tip of the snout to the anterior margin of the external naris yields a value of approximately 2.86 for the holotype of *Germanosaurus schafferi,* 2.7 for the holotype of *C. fridericianus,* and 3.0 for the neotype of *C. latifrons.* Dividing the longitudinal diameter of the upper temporal fossa by the longitudinal diameter of the orbit yields a value of 1.9 for the holotype of *Germanosaurus schafferi,* which falls into the upper range of variability of *Cymatosaurus* (1.3–2.0) and in between the range of variability between relatively plesiomorphic (*Nothosaurus marchicus*) and apomorphic (*Nothosaurus mirabilis*) representatives of the genus *Nothosaurus.* Indeed, the skull of *Germanosaurus schafferi* shows an intriguing combination of characters otherwise typical of *Cymatosaurus* or *Nothosaurus.*

The adult stage of *Germanosaurus* is indicated by the fusion of the premaxillae in the anterior part of the rostrum. The premaxilla meets the maxilla at the anterolateral edge of the external naris, in a suture that trends anterolaterally. In *Cymatosaurus* and *Nothosaurus,* the maxilla shows a distinct lateral bulging in the area between the external nares and orbits, which accommodates the roots of the paired maxillary fangs. In *Germanosaurus,* the lateral contours of the skull show a lateral bulging at the level of the external nares, but whereas the four, perhaps five, premaxillary teeth (fangs) are distinctly larger than the maxillary teeth, no maxillary fangs are observed either at the level of the lateral bulging of the maxilla

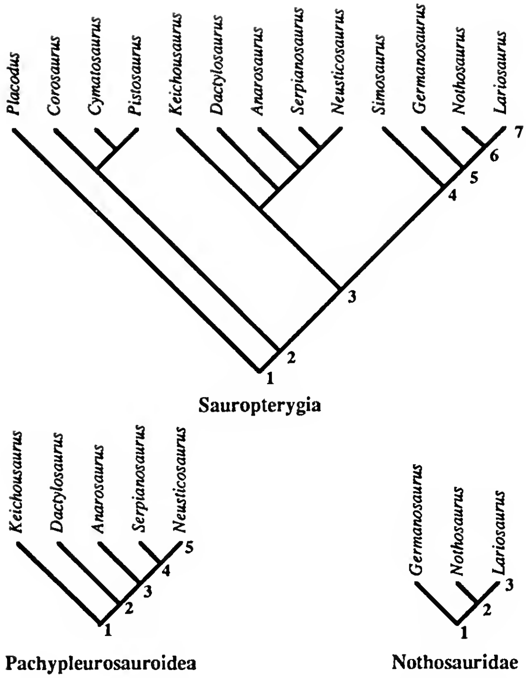

FIG. 15. Clade rank determination in Sauropterygia. Pachypleurosaur interrelationships are based on an independent study (Rieppel & Lin Kebang, 1995). For further discussion see text and Norell and Novacek (1992).

or behind it at the level between the external naris and the orbit. Because a small maxillary tooth is preserved (in the left maxilla) in the position where other Eosauropterygia carry paired maxillary fangs (between the external naris and the orbit), it is concluded that such fangs are absent in *Germanosaurus* (alternatively, one might assume that both fangs have been shed, and a replacement tooth is observed in situ, in which case the maxillary fangs would be a synapomorphy of the Nothosauridae rather than of the Nothosaurinae).

Germanosaurus differs from *Nothosaurus,* but resembles some specimens of *Cymatosaurus,* in that the nasals are reduced but still reach the posterior margin of the external nares. As in *Cymatosaurus,* but unlike *Nothosaurus,* there is no slender anterior process of the nasal lining the medial margin of the external naris that is defined by the premaxilla. Posteriorly, the nasals taper to a blunt tip that is embraced between an anterolateral and an anteromedial process of the frontal. At the level of the anterior margin of the orbit, the anteromedial process of the frontal meets the posterior (nasal) process of the premaxilla, which separates the nasals from one another. The anterolateral process of the frontal separates the nasal from the prefrontal.

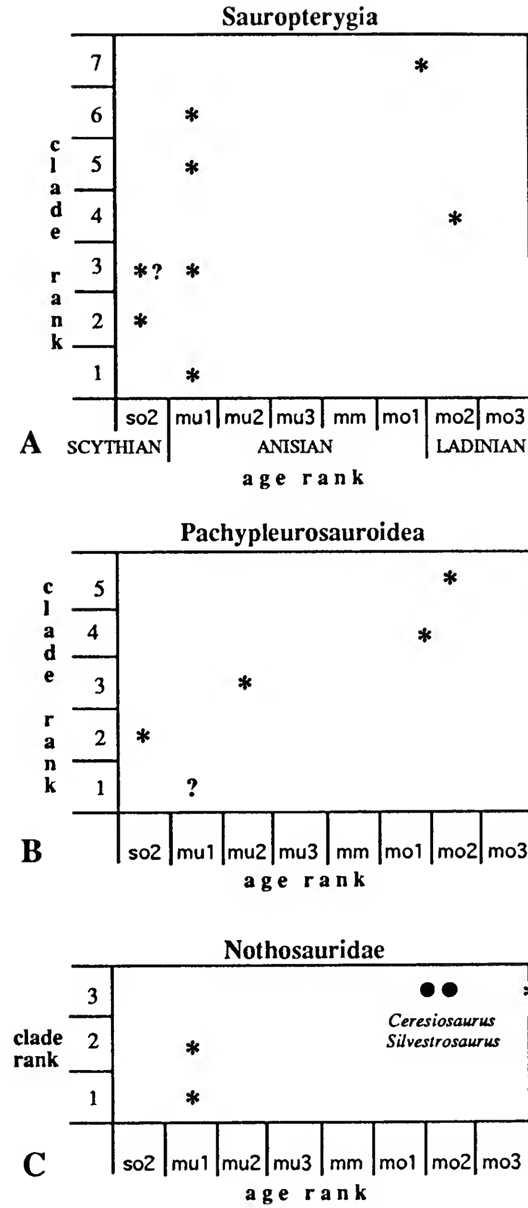

FIG. 16. Graphic representations of clade versus age rank for Triassic Sauropterygia (**A**), Pachypleurosauroidea, (**B**), and Nothosauridae (**C**). For further discussion see text.

As in *Nothosaurus,* but unlike *Cymatosaurus,* the dorsal exposure of the prefrontal is distinctly reduced. Yet, as in *Cymatosaurus* but unlike *Nothosaurus,* the frontals are paired. Since the prefrontal does not contact the postfrontal, the frontal

TABLE 3. Data matrix for the cladistic analysis of sauropterygian interrelationships. Character definitions are given in the Appendix. See Rieppel (1994a) and text for further discussion.

	1	1	2	3	4	5	6	7	8	9	10
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0	0	0	0	0	0	1	0 & 1
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	0	0	0	0	0	0	1	0
6	Kuehneosauridae	0	0	0	0	0	0	0	0	1	0
7	Rhynchocephalia	0	0	0	0	0	0	0	0	1 & 2	0
8	Squamata	0	0	0	0	0	0	0	0	1 & 2	0 & 1
9	Rhynchosauria	1	1	0	0	0	0	0	0	1	0
10	Prolacertiformes	1	1	0	0	1	0	0	0	1	0
11	Trilophosaurus	1	?	0	0	0	0	0	0	?	1
12	Choristodera	1	1	0	0	1	0	0	0	1	0
13	Archosauriformes	1	1	0	0	1	0	0	0	1	0
14	Claudiosaurus	0	0	0	0	0	0	0	0	1	0
15	Dactylosaurus	1	0	0	0	0	0	0	0	2	0
16	Serpiano-Neustico	1	0	0	0	0	0	0	0 & 1	2	0
17	Simosaurus	1	0	0	0	0	1	0	1	2	0
18	Nothosaurus	1	0	1	1	0	0	0	0 & 1	2	0
19	Lariosaurus	1	0	1	1	0	0	0	0 & 1	2	0
20	Corosaurus	1	0	0	0	0	0	0	0	2	0
21	Cymatosaurus	1	0	1	0	0	2	0 & 1	1	2	0 & 1
22	Germanosaurus	1	0	1	1	0	1	0	1	2	0
23	Pistosaurus	1	0	0	0	0	2	1	1	2	0
24	Placodus	1	0	1	0	1	0	0	0	2	1

broadly enters the dorsal (medial) margin of the orbit. Posteriorly, the frontals form well-defined posterolateral processes that embrace an anteromedial extension of the parietals. The exact location of the posterior tips of the frontals is difficult to ascertain due to damaged bone surface. Arthaber (1924, Fig. 11b) shows the posterolateral process of the frontal broadly entering the anteromedial margin of the upper temporal fossa. Closer inspection of the specimen indicates, however, that the parietal meets the postfrontal in a narrow suture along the anteromedial margin of the upper temporal fossa, thus excluding the frontal from the latter.

The postorbital arch is composed of the postfrontal and postorbital. The postfrontal defines the posterodorsal (-medial) margin of the orbit as well as the anteromedial margin of the upper temporal fossa. It shows a distinct postorbital constriction, as is also observed in some specimens of *Nothosaurus* (*N. marchicus*). The postorbital defines the posteroventral (-lateral) margin of the orbit and meets the squamosal in a broadly overlapping suture within the upper temporal arch. The anterior part of the postorbital is clearly delineated by a suture entering the posteroventral (-lateral) margin of the orbit.

At the level of the anterior margin of the postorbital, a distinct and deeply interdigitating suture trends laterally, marking the anterior end of the relatively broad jugal. This indicates that the ventral (lateral) margin of the orbit is formed by the maxilla and that the jugal remains excluded from the orbit as in most specimens of *Nothosaurus*, but unlike *Cymatosaurus*. The jugal extends posteriorly into the upper temporal arch lateral to the postorbital, but its exact delineation from the anterior process of the squamosal cannot be identified. An overlapping contact between the jugal and squamosal must be inferred from the general topology of the bones. The posterior end of the maxilla is difficult to identify in this incompletely

TABLE 3. Continued.

	2	11	12	13	14	15	16	17	18	19	20
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	?	0	0&2	0	0
3	Testudines	0	0&2	0	0	0	?	0	3	0	1
4	Araeoscelidia	0	1	1	0	1	0	0	0	0	0
5	Younginiformes	0	1	1	0	1	0	0	0	0	0
6	Kuehneosauridae	0	0	1	0	1	0	0	2	0	1
7	Rhynchocephalia	0	0	1	0&1	0&1	0	0&1	0&2	0&2	1
8	Squamata	0	0&1&2	1	0&1	0	0	0&1	0&2&3	0&2	1
9	Rhynchosauria	0	0	1	0	0	0	1	3	3	1
10	Prolacertiformes	0	1	1	0	0&1	0	0&1	2&3	0	1
11	Trilophosaurus	0	1	1	0	0	1	0	3	3	1
12	Choristodera	0	2	1	0	0	0	0	3	1	1
13	Archosauriformes	0	0&1	1	0&1	0&1	0&1&2	0&1	0&3	0&2	1
14	Claudiosaurus	0	1	1	0	1	0	0	0	0	1
15	Dactylosaurus	0	1	3	0	1	0	0	0	0	1
16	Serpiano-Neustico	0	1	3	0	1	0	0	0	0	1
17	Simosaurus	0	2	2	1	0	0	2	1	1	1
18	Nothosaurus	1	2	2	1	1	0	2	1	2&3	1
19	Lariosaurus	1	2	2	1	1	0	2	1	2	1
20	Corosaurus	0	0	1	0	1	1	0	0	1	1
21	Cymatosaurus	0	2	2	0	1	1&2	1&2	0	2&3	1
22	Germanosaurus	1	2	2	0	1	1	1	1	1	1
23	Pistosaurus	0	1	2	0	1	2	1	2	3	1
24	Placodus	0	0	2	0&1	1	0	0&2	2	0	1

prepared skull, but it appears to lie at the level of the anterior margin of the upper temporal fossa, where a suture between the jugal and maxilla is apparent.

The paired parietals form a skull table that is narrow but not as strongly constricted as is otherwise characteristic of *Cymatosaurus* or *Nothosaurus.* The pineal foramen is displaced posteriorly to a point distinctly behind the center of the skull table but still remaining at some distance from the posterior margin of the parietal skull table, as is the case in some early representatives of *Nothosaurus* (undescribed material from Winterswijk in private collections, and *N. marchicus*: Rieppel & Wild, 1996).

The occiput is only partially preserved and/or prepared. No sutures are apparent that would indicate the exact relationships of parietal and squamosal. A deep posterior excavation of the occiput is apparent from the outline of the skull, indicating posterolaterally trending paroccipital processes. No supraoccipital is exposed in dorsal view, as would be the case in *Nothosaurus,* which may indicate that the supraoccipital was more vertically oriented and/or only loosely connected to the dermatocranium as in *Cymatosaurus.*

The palatal view is not prepared in *Germanosaurus,* but through the left external naris the anterior margin of the internal naris is exposed, indicating the position of the internal naris, which lies relatively further back than is typical for *Nothosaurus,* but which corresponds to the position of the internal nares in *Cymatosaurus* (Table 1).

Cladistic Analysis

Earlier literature on the systematics of the genus *Cymatosaurus* placed much emphasis on the reduction of the nasals and their relation to the posterior margin of the external naris. In the most recent review of the genus, E.v. Huene (1944) recognized two subgenera, *Cymatosaurus* (*Cymato-*

TABLE 3. Continued.

	3	21	22	23	24	25	26	27	28	29	30
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	1	0	0	0	0	0	0	0	0	0
3	Testudines	1	0 & 1	0	0	0	?	0	1	0	0
4	Araeoscelidia	0	0	0	0	0	1	0 & 1	0	0	0
5	Younginiformes	0 & 1	0	0	0	0	1	1	0	0	0
6	Kuehneosauridae	1	1	0	0	0	1	2	1	1	1
7	Rhynchocephalia	1	0 & 1	0 & 1	1	0	1	1 & 2	0	0	1
8	Squamata	1	0 & 1	0 & 1	0	0	1	2	1	1	?
9	Rhynchosauria	1	1	0	1	0	1	1	1	0	0
10	Prolacertiformes	1	0 & 1	0	0 & 1	0	1	2	1	0 & 1	1
11	Trilophosaurus	1	?	0	?	0	1	0	?	0	?
12	Choristodera	1	1	0	0	0	1	1	1	0 & 1	0
13	Archosauriformes	1	0 & 1	0	1	0	1	1	1	0	0
14	Claudiosaurus	1	1	0	0	0	1	2	0	0	1
15	Dactylosaurus	1	1	?	0	0	2	2	0	0	1
16	Serpiano-Neustico	1	1	0	0	0	2	2	0	0	1
17	Simosaurus	1	1	0	0	1	1	2	0	0	1
18	Nothosaurus	1	1	1 & 2	0	1	1 & 2	2	0	0 & 1	1
19	Lariosaurus	1	1	1 & 2	0	1	2	2	0	?	?
20	Corosaurus	1	1	?	0	0	1	2	0	?	?
21	Cymatosaurus	1	1	1	0	0	1	2	0	1	?
22	Germanosaurus	1	1	2	0	1	1	2	0	?	?
23	Pistosaurus	1	1	?	0	1	1	2	0	1	?
24	Placodus	1	1	0	0	1	1	2	0	0	0

saurus) and *Cymatosaurus* (*Germanosaurus*). The first would be characterized by the exclusion of the nasals from the external nares (*erythreus, fridericianus, latifrons*), the second by the entry of the nasals into the external nares (*silesiacus, gracilis* [in Schrammen's, 1899, first specimen, but not in his second specimen; see above], *latissimus, schafferi*). The description of the currently available material shows a high degree of incongruence of this with other characters, such as the contact of the pre- and postfrontal at the dorsal margin of the orbit, entry of the frontal into the anteromedial margin of the upper temporal fossa, the number of maxillary teeth preceding the maxillary fangs, and the relative width of the dorsal bridge between the orbits. To test the monophyly of the two subgenera recognized by E.v. Huene (1944), a small data matrix (Table 2) was constructed for the following characters:

1. Nasals entering (0) or excluded from (1) the posterior margin of the external naris.
2. Prefrontal and postfrontal do not (0) or do (1) meet along the dorsal margin of the orbit.
3. The frontal does not (0) or does (1) enter the anteromedial margin of the upper temporal fossa.
4. Three (0) or one (1) maxillary tooth preceding paired maxillary fangs.
5. Dorsal bony bridge between orbits larger (0) or smaller (1) than twice the width of the dorsal bridge between the external nares.

The data were analyzed using the software package PAUP version 3.1.1. developed by David L. Swofford (Swofford, 1990; Swofford & Begle, 1993). The branch-and-bound search for the shortest unrooted network (character 4 uninformative and hence ignored in the analysis) among all the previously described and currently available skulls of *Cymatosaurus* (9 terminal taxa, Table 2) yields a total of 57 most parsimonious trees (MPTs) with a tree length (TL) of 5 steps, a consistency index (CI) of 0.8, and a retention index

TABLE 3. Continued.

	4	31	32	33	34	35	36	37	38	39	40
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	?	0	0	0	0	0	0
3	Testudines	0	0	0&2	0	0	0	1	1	0	0
4	Araeoscelidia	0	0	0	1	0	0	0	0	?	0
5	Younginiformes	0	0	0	1	0	0	1	1	?	0
6	Kuehneosauridae	0	0	0	1	0	1	1	1	?	1
7	Rhynchocephalia	0&1	0	0	1	0	0&1	1	1	1	0&1
8	Squamata	0	0	0&1&2	0&1	0&1	0&1	1	1	1	1
9	Rhynchosauria	1	0	0	0	0	0	1	1	1	0
10	Prolacertiformes	1	0	0	1	0	0	1	1	?	0
11	Trilophosaurus	1	0	2	?	0	?	1	1	0	0
12	Choristodera	1	0	1	1	0	1	1	1	?	0
13	Archosauriformes	0&1	0	0&1&2	1	0	0&1	1	1	?	0
14	Claudiosaurus	0	0	0	?	0	0	0	0	?	0
15	Dactylosaurus	2	0	0	?	1	0	1	1	1	0
16	Serpiano-Neustico	2	0	0	?	1	0	1	1	1	0
17	Simosaurus	2	0	1	1	0	0	0	1	0	0
18	Nothosaurus	2	0	0&1	1	1	1	0	1	0	0
19	Lariosaurus	2	0	0	?	1	1	0	1	0	0
20	Corosaurus	1	1	1	1	0	1	0	1	1	0
21	Cymatosaurus	1	1	1	?	0	0&1	0	1	?	0
22	Germanosaurus	?	?	?	?	?	0	0	1	?	0
23	Pistosaurus	1	?	1	?	0	1	0	1	1	0
24	Placodus	1	0	0	1	0	0	1	1	1	0

(RI) of 0.833. The strict consensus tree shows no resolution except for a pairing of *latissimus* with Schrammen's (1899) first specimen of *gracilis.* The character that links these two taxa in the unrooted network is the absence of a contact of pre- and postfrontal at the dorsal margin of the orbit, a plesiomorphy compared to outgroups (pachypleurosaurs, *Simosaurus,* Nothosauridae). If the branch-and-bound analysis is rooted on an all-0 ancestor (assuming monophyly of the genus *Cymatosaurus*), all characters become informative. The branch-and-bound search yields a total of 383 MPTs (TL = 7, CI = 0.714, RI = 0.75), with a strict consensus tree that shows absolutely no resolution among the terminal taxa. It is therefore concluded that there is no evidence for the monophyly of the subgenera recognized by E.v. Huene (1944). In fact, cladistic analysis at a more global scale indicates that a taxon comprising *Cymatosaurus* and *Germanosaurus* is nonmonophyletic.

A global assessment of the phylogenetic relationships of the genera *Cymatosaurus* and *Germanosaurus* within the Sauropterygia was based on the data matrix used in an earlier analysis of sauropterygian interrelationships (see Rieppel, 1994a, for an extensive discussion of characters and for references). The data matrix was substantially expanded, and some characters used earlier were redefined following the study of all original material of *Cymatosaurus* and *Germanosaurus* deposited in public repositories and after further preparation of the type material of *Corosaurus* from the Alcova Limestone of Wyoming (Storrs, 1991). Character definitions are given in the Appendix; the coding of characters is given in Table 3. A full discussion of the characters will appear elsewhere, in conjunction with a redescription of *Corosaurus.* Discussion of characters will here be restricted to those relevant in the study of *Cymatosaurus* and *Germanosaurus.*

Simosaurus was recoded for character 6(1) in view of the fact that the nasals are as much reduced in this genus as they are in *Germanosaurus,* a degree of reduction that is intermediate between

TABLE 3. Continued.

	5	41	42	43	44	45	46	47	48	49	50
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	1	0	0	0	0
3	Testudines	0&1	0	1	0	0&1	1	0	0&1	0	0
4	Araeoscelidia	0	0	1	0	0	0	0	0	0	0
5	Younginiformes	0	0	1	0	0	0	0	1	1	0
6	Kuehneosauridae	0	0	1	0	?	?	0	1	0	0
7	Rhynchocephalia	0	0	1	0	0	0	0	1	1	0
8	Squamata	0	0	1	0	0&1	0	0	1	1	0
9	Rhynchosauria	0	0	1	0	1	0	0	1	1	0
10	Prolacertiformes	0	0	1	0	0	0	0	1	0&1	0
11	Trilophosaurus	0	0	1	0	0	0	0	1	1	0
12	Choristodera	?	0	1	0	1	0	0	1	0	0
13	Archosauriformes	0&1	0	1	0	0&1	0&1	0	1	0&1	0
14	Claudiosaurus	0	0	1	1	0	0	0	0	0	?
15	Dactylosaurus	1	?	0	1	0	1	?	1	0	0
16	Serpiano-Neustico	1	?	0	1	0	1	?	1	0	0
17	Simosaurus	1	2	0	1	0	0	1	1	0	1
18	Nothosaurus	1	2	0	0&1	1	0	1	1	0	1
19	Lariosaurus	1	?	0	1	?	0	?	1	0	1
20	Corosaurus	1	?	0	0	?	0	?	1	1	1
21	Cymatosaurus	1	?	0	0	1	0	1	?	0	?
22	Germanosaurus	1	?	?	?	?	?	?	?	?	?
23	Pistosaurus	1	?	0	0	?	0	?	?	?	?
24	Placodus	1	1	0	0	1	0	0	1	1	0

the plesiomorphic condition and the one seen in *Cymatosaurus* and *Pistosaurus*. *Cymatosaurus* was recoded for character 19(2&3) in view of an as yet undescribed species from the lower Muschelkalk of Thuringia that shows a sagittal crest (Rieppel & Werneburg, in prep.). The fact that the braincase (except for the basicranium in the undescribed specimen from the lower Muschelkalk of Thuringia) is missing in all specimens of *Cymatosaurus* available today resulted in recoding characters 31(0) and 32(1) for *Cymatosaurus*. Attention is also drawn to the occiput of the specimen BGR S 44/3 (Fig. 3B), which shows a distinct notch in the lower margin of the occipital exposure of the squamosal. A similar notch receives the distal end of the paroccipital process in a loose articulation in *Corosaurus*. Preservation of the basicranium in the undescribed specimen from the lower Muschelkalk of Thuringia also documents an akinetic palate for *Cymatosaurus* (character 41[1]) in spite of the otherwise loose connection of the braincase with the dermatocranium and the reconstruction of the passage of the internal carotid in this genus (character 47; see also Rieppel, 1994b). Characters for the postcranial skeleton of *Cymatosaurus* were coded and/or added on the assumption that *Proneusticosaurus* Volz, 1902, is a junior synonym of the first genus (Sues, 1987; Rieppel & Hagdorn, 1996).

In an initial PAUP analysis, all Sauropterygia were treated as ingroup taxa (presumed monophyletic); the Captorhinidae, Testudines, Araeoscelidia, Younginiformes, and *Claudiosaurus* were used as outgroup (paraphyletic). All other taxa were deleted from the analysis, rendering characters 2, 5, 24, 28, 34, 40, 53, 63, 66, 111, and 117 uninformative (ignored). All multistate characters were treated as unordered except for character 27, which was ordered because presence of a lower temporal opening must logically precede the loss of the lower temporal arcade (see also Rieppel, 1994a). Heuristic search options included random stepwise addition and branch swapping (on minimal trees only) by tree bisection and re-

TABLE 3. Continued.

	6	51	52	53	54	55	56	57	58	59	60
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	?	0	0	0	0	0
3	Testudines	0	1	?	?	?	?	?	0	0&1	0&2
4	Araeoscelidia	0	1	0	0	0	0	0	0	0	0
5	Younginiformes	0	?	0	0	0	1	0	0	0	0
6	Kuehneosauridae	0	?	0	0	0	1	0	1	1	0
7	Rhynchocephalia	0	1	1	0	0	1	0	1	0&1	0
8	Squamata	0	1	1	0	0	1	0	1	1	0&2
9	Rhynchosauria	0	0	0	?	0	1	0	1	1	0
10	Prolacertiformes	0	1	0	0	0	1	0	0&1	1	0&2
11	Trilophosaurus	0	?	0	?	0	1	0	1	1	1&2
12	Choristodera	0	1	0	0	0	1	0	0	1	1
13	Archosauriformes	0	1	0	0	0	1	0	0&1	1	0&1&2
14	Claudiosaurus	0	1	0	0	0	1	0	0	?	0
15	Dactylosaurus	0	?	0	0	0	1	0	1	1	0
16	Serpiano-Neustico	0	?	0	0	0	1	0	1	1	0
17	Simosaurus	0	1	0	1	0	1	2	1	1	1
18	Nothosaurus	2	1	0	1	1	0	2	1	1	1
19	Lariosaurus	2	?	0	1	1	0	2	1	1	1
20	Corosaurus	1	?	0	1	1	0	1	1	1	0
21	Cymatosaurus	2	1	0	1	1	0	1	1	1	1
22	Germanosaurus	?	?	0	1	1	1	1	?	?	?
23	Pistosaurus	?	?	0	1	1	0	1	1	1	1
24	Placodus	2	0	0	1	0	1	0	1	0	0

connection. One hundred replications yielded two MPTs with a TL of 283 steps, a CI of 0.675, and an RI of 0.702. The strict consensus tree of the two MPTs (Fig. 13) shows lack of resolution among outgroup taxa. Sauropterygian relationships are fully resolved, however, and differ significantly from previous results (Rieppel, 1994b). The emendation of the data matrix results in full resolution of the interrelationships of the genera *Cymatosaurus, Lariosaurus, Nothosaurus,* and *Pistosaurus,* which formed an unresolved polytomy in the previous analysis (Rieppel, 1994a, Fig. 67). Moreover, the analysis reveals paraphyly of the Eusauropterygia *sensu* Tschanz (1989), as it dramatically changes the position of pachypleurosaurs (see Fig. 13 and discussion below).

Identical sauropterygian interrelationships result from a more encompassing analysis that treats all 23 taxa in the analysis (see Table 3) as monophyletic ingroup (Reptilia), rooted on an all-0 ancestor. All characters are informative. Heuristic search settings were the same as before, again with character 27 as the only ordered multistate character, with random stepwise addition, and with branch swapping (on minimal trees only) by tree bisection and reconnection. One hundred replications yielded two MPTs, with a TL of 452 steps, a CI of 0.648, and an RI of 0.711. The strict consensus tree (Fig. 14) shows lack of resolution to be restricted to the interrelationships among archosauromorph taxa; all other taxa are fully resolved. Testudines remains the sister-group of the Sauropterygia, with the Lepidosauria as sister-group of the two. Interrelationships within the Sauropterygia are completely resolved, as was the case in the previous analysis using selected outgroup taxa only. *Placodus* remains the sister-taxon of all other sauropterygians, the Eosauropterygia (Rieppel, 1994a), whereas the Eusauropterygia *sensu* Tschanz (1989) are, again, paraphyletic. In contrast to the earlier analysis, the new data basis shows the Eosauropterygia to subdivide into two major clades. The basal clade (of the ladderized cladogram in Fig. 14) comprises the genera (*Co-*

TABLE 3. Continued.

	7	61	62	63	64	65	66	67	68	69	70
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	?	0	0	0	0	0
3	Testudines	1	0&1	1	0	0	0	0	0	0	0
4	Araeoscelidia	0	0	1	0	?	0	0	0	0	0
5	Younginiformes	0	0	1	0	0	0	0	0	0	0
6	Kuehneosauridae	1	1	1	0	?	1	0	0	0	1
7	Rhynchocephalia	0&1	0	1	1	0	0	0	0	0	0
8	Squamata	1	0	1	0&1	0	0	0	0	0	0&1
9	Rhynchosauria	0	0	1	0	?	0	0	0	0	0&1
10	Prolacertiformes	0&1	0&1	1	0	?	0	0	0	0	0
11	Trilophosaurus	0	0	1	0	?	0	?	0	0	0
12	Choristodera	1	0	1	0	1	0	0	0	0	0
13	Archosauriformes	0&1	0&1	1	0	0	1	0	0	0	0&1
14	Claudiosaurus	0	0	1	0	?	0	0	0	0	0
15	Dactylosaurus	1	1	1	1	1	0	1	0	1	0
16	Serpiano-Neustico	1	1	1	1	1	0	1	0	1	0
17	Simosaurus	1	1	1	1	1	0	0	0	0	1
18	Nothosaurus	1	1	1	1	1	0	1	0	0&1	0
19	Lariosaurus	1	1	1	?	?	0	1	0	1	0
20	Corosaurus	1	1	1	0	1	0	0	1	0	1
21	Cymatosaurus	1	1	?	1	1	0	0	0	?	?
22	Germanosaurus	?	?	?	?	?	?	?	?	?	?
23	Pistosaurus	?	?	?	1	1	0	0	1	0	?
24	Placodus	1	1	1	0	0	1	0	0	0	1

rosaurus, (*Cymatosaurus, Pistosaurus*)), and it is the sister-group of a clade that includes pachypleurosaurs, *Simosaurus, Germanosaurus*, and the *Nothosaurus–Lariosaurus* clade. In contrast to previous results (Rieppel, 1994a), both *Corosaurus* and pachypleurosaurs are nested within the Eusauropterygia *sensu* Tschanz (1989). The monophyletic pachypleurosaurs (*Dactylosaurus* and the *Serpianosaurus–Neusticosaurus* clade) form the sister-group of a nothosaurian clade that includes the sequential sister-taxa (*Simosaurus*, (*Germanosaurus*, (*Nothosaurus, Lariosaurus*))).

Sauropterygian interrelationships remain unchanged in a tree one step longer than the two MPTs (TL = 453). A tree two steps longer (TL = 454) conserves the monophyly of pachypleurosaurs, of the *Germanosaurus–Nothosaurus–Lariosaurus* clade, and of the *Corosaurus–Cymatosaurus–Pistosaurus* clade, but the three clades fall into an unresolved polytomy with *Placodus*. In a tree three steps longer (TL = 455), only the monophyly of the *Corosaurus–Cymatosaurus–Pistosaurus* and of the *Germanosaurus–Nothosaurus–Lariosaurus* clades is conserved beyond the monophyly of the Sauropterygia. A tree four steps longer (TL = 456) retains monophyly of the Sauropterygia only. Bootstrap support values (1,000 replications) are 100% for the monophyly of the Sauropterygia, 94% for the monophyly of pachypleurosaurs (*Dactylosaurus* and the *Serpianosaurus–Neusticosaurus* clade), 92% for the sister-group relationship of *Nothosaurus* and *Lariosaurus*, 60% for the monophyly of the Eosauropterygia, 51% for the monophyly of the (*Corosaurus*, (*Cymatosaurus, Pistosaurus*)) clade, 56% for the (*Simosaurus*, (*Germanosaurus*, (*Nothosaurus Lariosaurus*))) clade, 53% for the (*Germanosaurus*, (*Nothosaurus, Lariosaurus*)) clade, and 53% for the sister-group relationship of *Cymatosaurus* and *Pistosaurus*.

The implementation of DELTRAN character optimization will minimize the number of synapomorphies diagnostic at any node that will subsequently be lost again within that same clade. For

TABLE 3. Continued.

	8	71	72	73	74	75	76	77	78	79	80
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	?	0	0	0	0
3	Testudines	0	0	0	0	0	1	0	0	0	0
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	0	0	0&1	0&1	1	0	0	0
6	Kuehneosauridae	?	0	0	0	1	?	?	?	?	?
7	Rhynchocephalia	0	0	0	0	1	1	1	0	0	0
8	Squamata	0	0	0	0	1	1	0&1	0	0	0
9	Rhynchosauria	0	0	0	0	0	1	1	0	0	0
10	Prolacertiformes	1	0	0	0	1	1	1	0	0	0
11	Trilophosaurus	1	0	0	0	?	1	1	0	0	0
12	Choristodera	1	0	1	0	0	1	1	1	0	0
13	Archosauriformes	1	0	0&2	0	0&1	1	1	0	0	0
14	Claudiosaurus	1	0	0	0	1	1	1	0	0	0
15	Dactylosaurus	1	0	1	1	0	1	0	1	1	1
16	Serpiano-Neustico	1	1	1	1	0	1	0	1	1	0
17	Simosaurus	1	0	1	0	0	1	0	1	1	1
18	Nothosaurus	1	0&1	1	1	0&1	1	0&1	1	1	1
19	Lariosaurus	1	0&1	2	1	0	1	0	1	1	1
20	Corosaurus	1	0	1	0	1	1	1	1	0	1
21	Cymatosaurus	?	0	?	?	0	1	?	?	?	?
22	Germanosaurus	?	?	?	?	?	1	?	?	?	?
23	Pistosaurus	1	0	?	?	?	1	?	?	?	?
24	Placodus	1	0	1	0	0	1	1	1	0	0

that reason, it will generally indicate synapomorphic characters (character states) at a level of minimal inclusiveness (rather than maximal inclusiveness, as an ACCTRAN character optimization would). Taxa are here diagnosed on the basis of DELTRAN character optimization. The synapomorphies linking *Cymatosaurus* with *Pistosaurus* are the following: 6(2) nasals strongly reduced or absent (CI = 0.667); 8(1) nasals (always) separated by premaxilla–frontal contact (CI = 0.8); 16(2) frontal enters anteromedial margin of upper temporal fossa (CI = 0.714, reversed in some *Cymatosaurus*); 17(1) parietal fused in their posterior part only (CI = 0.8); 19(3) parietal forming a sagittal crest (CI = 0.727, reversed in some *Cymatosaurus*); 29(1) quadratojugal absent (CI = 0.667); 60(1) vertebrae platycoelous (CI = 0.7); 64(1) zygosphene–zygantrum articulation present (CI = 0.5). Unequivocal synapomorphies (out of a total of nine characters supporting the node) shared by *Corosaurus* and the *Cymatosaurus–Pistosaurus* clade are the notch on the squamosal for articulation with the distal end of the paroccipital process (32[1]) and the distal expansion of the posterodorsal process of the scapula (85[1]). Under the new phylogenetic hypothesis of sauropterygian interrelationships, the open occiput in *Corosaurus, Cymatosaurus,* and *Pistosaurus* (and by extension, in plesio- and pliosaurs) is a plesiomorphic trait rather than a reversal.

Unequivocal synapomorphies (CI = 1; out of a total of nine characters supporting the node) shared by pachypleurosaurs and the (*Simosaurus* (*Germanosaurus* (*Nothosaurus, Lariosaurus*))) clade are the clavicles which meet in an anteromedial suture (79[1]), and the strongly waisted coracoid (88[2]). *Simosaurus* shares with the Nothosauridae a total of 16 synapomorphies, among which are the following: the posteriorly displaced pineal foramen (18[1]), the broad dorsal wing of the epipterygoid (39[0]; unknown for *Germanosaurus*), the complex lateral relations of the basioccipital tubers (42[2]; unknown for *Germanosaurus* and *Lariosaurus*), the extension of the

TABLE 3. Continued.

	9	81	82	83	84	85	86	87	88	89	90
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	?	0	?	0	1	0	0	0
3	Testudines	0	1	0	0	?	?	0	0	1	0
4	Araeoscelidia	0	1	0	0	?	0	1	0	0	0
5	Younginiformes	0	0&1	0	0	?	1	0	0	0	0
6	Kuehneosauridae	?	?	?	1	?	1	0	0	0	0
7	Rhynchocephalia	0	1	0	0	?	1	0	0	0	0
8	Squamata	0	1	0&1	0	?	1	0	0	0	0
9	Rhynchosauria	0	1	0	0	?	1	0	0	0&1	0
10	Prolacertiformes	0	0	?	0	?	1	0	0	0	0
11	Trilophosaurus	0	1	0	0	?	1	0	0	0	0
12	Choristodera	0	1	0	0	?	1	0	0	0	0
13	Archosauriformes	0	1	0	0	?	1	0	0	0&1	0
14	Claudiosaurus	0	1	0	0	?	1	0	0	0	0
15	Dactylosaurus	1	?	?	1	0	1	0	2	1	1
16	Serpiano-Neustico	1	0&1	2	1	0	1	0	2	1	1
17	Simosaurus	1	1	1	1	0	1	0	2	1	1
18	Nothosaurus	1	0&1	2	1	0	1	0	2	1	1
19	Lariosaurus	1	?	?	1	0	1	0	2	1	1
20	Corosaurus	1	1	1	1	1	1	0	1	1	1
21	Cymatosaurus	?	?	?	?	?	?	0	?	?	?
22	Germanosaurus	?	?	?	?	?	?	0	?	?	?
23	Pistosaurus	?	?	?	1	1	1	0	3	?	?
24	Placodus	1	1	1	0	?	1	0	0	1	1

maxillary tooth row to a level below the upper temporal fossa (57[2]; reversed in *Germanosaurus*), the reduced posterior process on the ilium (99[2], unknown in *Germanosaurus*), and the concave ventral (medial) margin of the pubis (100[1], unknown in *Germanosaurus*).

Synapomorphies of the Nothosauridae, shared by *Germanosaurus* and the Nothosaurinae (*Nothosaurus* and *Lariosaurus*), are the following: 3(1) snout constricted (CI = 0.333); 4(1) temporal region of skull strongly depressed (CI = 1); 11(1) reduced dorsal exposure of prefrontal (CI = 1); 23(2) jugal restricted to position behind orbit without entering its posterior margin (CI = 1; rarely reversed in individuals of *Nothosaurus*); 55(1) premaxillary and anterior dentary fangs present (CI = 0.5). The Nothosaurinae (*Nothosaurus* and *Lariosaurus*) finally share eight synapomorphies, that is, the fused frontals (14[1]), the strongly constricted parietal skull table (19[2]), the horizontal position of the supraoccipital (35[1]), the presence of an occipital crest (36[1]), the strongly elongated mandibular symphysis (51[2]), the presence of paired fangs in the maxilla (56[0]), the unconstricted vertebral centra (67[1]), and the absence of a distal expansion on the sacral ribs (74[1]). Several of these characters are convergent in *Cymatosaurus*.

Phylogenetic Pattern and Stratigraphic Superposition

With a more resolved cladogram of sauropterygian interrelationships at hand, a comparison of stratigraphic superposition (age rank) of taxa with their position in the cladogram (clade rank) becomes possible. Clade rank (Fig. 15) was determined following the method outlined by Norell and Novacek (1992). Calibration of age rank (Fig. 16) is here based on the stratigraphy of the Germanic Triassic (so, Röt, upper Buntsandstein; mu, lower Muschelkalk; mm, middle Muschelkalk;

TABLE 3. Continued.

	10	91	92	93	94	95	96	97	98	99	100
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0	0	0&1	0&2	1	0	1&2	0
4	Araeoscelidia	1	0	0	0	0	0	0	0	0	0
5	Younginiformes	1	0	0	0	0	0&2	0	0&1	0	0
6	Kuehneosauridae	1	0	0	0	0	2	1	2	0	0
7	Rhynchocephalia	1	0	0	0	0	2	0	0	0	0
8	Squamata	1	0	0	0	0	0&2	1	0	0	0
9	Rhynchosauria	1	0	0	0	0	0	1	0	0	0
10	Prolacertiformes	1	0	0	0	0	0	1	1&2	0	0
11	Trilophosaurus	1	0	0	?	0	0	1	0	0	0
12	Choristodera	1	0	0	0	0	0&2	1	2	0	0
13	Archosauriformes	1	0	0	0	0&1	0	1	0	0	0
14	Claudiosaurus	0	0	1	1	1	1	0	0	0	0
15	Dactylosaurus	0	1	0	1	0	0	0	1	3	0
16	Serpiano-Neustico	0	1	0	1	0&1	0&1	0	1&2	3	0&1
17	Simosaurus	0	1	0	1	1	1	1	2	2	1
18	Nothosaurus	0	1	0&1	0&1	1	0&1	0	2	2	1
19	Lariosaurus	0	1	1	1	1	1	0	2	3	0&1
20	Corosaurus	0	1	1	1	1	0	0	2	1	0
21	Cymatosaurus	0	0	0	0	0	0	0	?	?	0
22	Germanosaurus	?	?	?	?	?	?	?	?	?	?
23	Pistosaurus	0	1	?	1	1	1	1	2	0	?
24	Placodus	0	1	1	1	1	0	1	2	1	0

mo, upper Muschelkalk). The boundary between Spathian (upper Scythian, upper Lower Triassic) and Anisian (lower Middle Triassic) corresponds to the boundary between Buntsandstein (so_2) and Muschelkalk (mu_1). The boundary between Anisian and Ladinian corresponds to the boundary between mo_1 and mo_2 in the upper Muschelkalk. A full discussion of stratigraphic correlations for sauropterygians from the Germanic and Alpine Triassic can be found in Rieppel and Hagdorn (1996).

Looking at the Sauropterygia as a whole (Fig. 16A), nonresolution is evident, that is, a distinct clumping of the fossil record in the upper Spathian (Röt) and lower Anisian (lower Muschelkalk). The earliest record for *Placodus* (clade rank 1), and indeed for Placodontia as a whole in European epicontinental deposits (Rieppel, 1995b), is from the lower Gogolin Beds (basal mu_1) in Upper Silesia (Meyer, 1851b; Huene, 1905) and, thus, perhaps slightly younger than the occurrence of *Corosaurus* (clade rank 2) in the upper Scythian of North America (Storrs, 1991, 1993a; the Alcova limestone that yielded *Corosaurus* is believed to represent an "uppermost Lower Triassic or Scythian (Spathian) rock unit, or perhaps lowermost middle Triassic or Anisian"; Storrs, 1991; p. 101). The first occurrence of *Cymatosaurus* is in the upper Buntsandstein (so_2, Röt) of Rüdersdorf near Berlin. The first occurrence of *Placodus* is also slightly younger than that of pachypleurosaurs, which in the Germanic Triassic may reach back to the upper Buntsandstein (so_2, Röt) (*Dactylosaurus* [clade rank 3]; see Rieppel & Lin, 1995). Unfortunately, the stratigraphic control over the occurrence of *Keichousaurus* in China is not as precise as the data available for the Muschelkalk fossils. The first occurrence of Nothosauridae (age rank 5) again is in the lower Gogolin Beds (basal mu^1) of Upper Silesia (Kunisch, 1888; Rieppel & Wild, in press) and, hence, different from the age rank attributed to these taxa by Storrs (1993b, Fig. 5), who shows "Nothosauridae" to appear later than *Placodus* and pa-

TABLE 3. Continued.

	11	101	102	103	104	105	106	107	108	109	110
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	1	0	0	0	0	1	1	1	0
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	1	1	0	1	0	1	0	0
6	Kuehneosauridae	0	1	1	1	0	1	0	1	?	0
7	Rhynchocephalia	0	1	1	1	0	1	0	1	1	0
8	Squamata	0	1	1	1	0	1	0	1	1	0
9	Rhynchosauria	0	0	1	1	0	1	0	1	1	0
10	Prolacertiformes	0	0&1	1	1	0	1	0	1	0	0
11	Trilophosaurus	0	0	1	1	0	1	0	1	0	0
12	Choristodera	0	0	1	1	0	1	1	1	?	0
13	Archosauriformes	0	0	1	1	0	1&2	0&1	1	0	0
14	Claudiosaurus	0	0	1	1	0	1	1	1	0	0
15	Dactylosaurus	0	1	1	?	1	?	?	?	?	0
16	Serpiano-Neustico	0&1	1	1	1	1	2	1	1	1	1
17	Simosaurus	0	1	1	1	1	2	1	1	1	1
18	Nothosaurus	0	1	1	1	1	2	1	1	1	1
19	Lariosaurus	1	1	1	1	1	2	1	1	1	1
20	Corosaurus	1	1	1	1	0	1	1	1	1	0
21	Cymatosaurus	1	1	1	1	0	1	1	1	?	?
22	Germanosaurus	?	?	?	?	?	?	?	?	?	?
23	Pistosaurus	?	?	?	1	1	?	?	?	?	?
24	Placodus	0	1	1	1	0	1	1	1	1	0

chypleurosaurs to appear later than "Nothosauridae." Taxa that escape the clumping around the late Lower Triassic and early Middle Triassic are the late-appearing *Simosaurus* (upper Muschelkalk, mo_2; clade rank 4) and *Lariosaurus* (here considered to include *Silvestrosaurus* and *Ceresiosaurus,* and hence with a first occurrence at the Anisian–Ladinian boundary; clade rank 7). *Pistosaurus* is another late occurrence in the upper Muschelkalk (mo_1) of Bayreuth. As noted by Storrs (1993a), these late occurrences highlight the incompleteness of the fossil record for the Sauropterygia. The late appearance of *Simosaurus,* and its restriction to the Ladinian of the southern Germanic Basin and of the northern Alps, is particularly problematic, because cladistic analysis shows this taxon to be the sister-group to the Nothosauridae, with both *Germanosaurus* and *Nothosaurus* appearing in the basal Muschelkalk. Jaw fragments described as *Hemilopas* by Meyer (1851a) from the basal middle Muschelkalk could perhaps represent an early simosaurid, partially bridging the stratigraphic gap highlighted by cladistic analysis (Rieppel, 1995a). Alternatively, the clade rank of *Simosaurus* might change following the study of Chinese material (*Shingyisaurus* Young, 1965).

The clumping of sauropterygian taxa at the transition from the Lower to the Middle Triassic (Fig. 16A) appears to be an effect of sampling bias, as it correlates with marine transgressions that started in late Spathian times and persisted from early Anisian through Ladinian times and that induced the formation of the Röt (upper Lower Triassic) and Muschelkalk (Middle Triassic) sediments in Europe (Hagdorn, 1991). The comparison of age rank and clade rank in Sauropterygia presented in this study seems to highlight the early immigration of these taxa into the newly formed epicontinental sea, rather than the rapid and early diversification of the Sauropterygia within this emerging ecosystem. This conclusion is in accordance with the observation that all earliest occurrences of European taxa are in the east-

TABLE 3. Continued.

	12	111	112	113	114	115	116	117	118	119
1	Ancestor	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0&1	1	0	1	1	0	?
4	Araeoscelidia	0	1	0	0	0	0	0	1	0
5	Younginiformes	0	1	0	0	0	1	0	1	0
6	Kuehneosauridae	?	?	?	?	?	?	?	?	?
7	Rhynchocephalia	0	1	0&1	1	0	1	1	1	0
8	Squamata	0	1	1	1	0	1	1	1	?
9	Rhynchosauria	1	1	0	1	0	1	1	?	0
10	Prolacertiformes	0&1	1	0&1	1	0	1	0&1	1	0
11	Trilophosaurus	1	1	0	1	0	1	1	?	?
12	Choristodera	1	1	0	1	0	1	1	?	?
13	Archosauriformes	1	1	0&1	1	0	1	1	1	0
14	Claudiosaurus	0	1	0	0	0	0	0	?	0
15	Dactylosaurus	?	?	?	?	?	?	?	0	0
16	Serpiano-Neustico	0	0	1	1	2	0	0	0	0
17	Simosaurus	0	0	1	1	1	0	0	0	1
18	Nothosaurus	0	0	1	1	1	0	0	0	1
19	Lariosaurus	0	0	1	1	0	0	0	0	0
20	Corosaurus	0	0	1	1	1	?	?	0	1
21	Cymatosaurus	?	?	?	?	?	?	?	0	0
22	Germanosaurus	?	?	?	?	?	?	?	0	?
23	Pistosaurus	?	?	?	?	?	?	?	0	?
24	Placodus	0	0	1	1	2	0	0	0	0

ern part of the Germanic Basin, which is believed to have been connected to the Paleotethys through the East Carpathian gate (Kozur, 1974; Hagdorn, 1985; Urlichs & Mundlos, 1985), and also with the fact that some sauropterygians with low clade rank occur in the late Lower Triassic or early Middle Triassic outside Europe (*Corosaurus* in the western United States, and Placodontia and Eusauropterygia in Israel and China; Storrs, 1991; Brotzen, 1957; Young, 1959, 1960, 1965, 1978). This does not exclude the possibility that some sauropterygian taxa originated in the western Tethyan province, such as nothosaurian subclades (*Lariosaurus*).

Analysis of pachypleurosaurs in isolation, however, yields a different picture altogether (Fig. 16B, based on a comprehensive review of the phylogenetic interrelationships of the group; Rieppel & Lin, 1995). Clade rank 1 is assigned to the Chinese genus *Keichousaurus,* whose exact stratigraphic provenience within the Middle (or upper Lower?) Triassic is not known. Clade rank 2 is assigned to *Dactylosaurus* from the lowermost Muschelkalk, perhaps upper Buntsandstein (Röt). *Anarosaurus* from the uppermost lower Muschelkalk and from the basal middle Muschelkalk is assigned clade rank 3. *Serpianosaurus* from the Anisian–Ladinian boundary ranks fourth in the cladogram and is followed in time by *Neusticosaurus* with clade rank 5. For pachypleurosaurs at least, there exists a high degree of correlation between phylogenetic pattern and stratigraphic superposition, suggesting an eastern Tethyan origin of the clade, and a diversification of the clade within the western Tethyan province.

For the Nothosauridae, the two basal clades ranking 1 (*Germanosaurus*) and 2 (*Nothosaurus*) both appear in the lowermost Muschelkalk of Upper Silesia. The late occurrence of *Lariosaurus s.s.* seems to point to a significant gap in the fossil record, which is partly bridged by the synonymy of the genera "*Silvestrosaurus*" and "*Ceresiosaurus*" (solid dots in Fig. 16C) with *Lariosaurus.* Revision of the monophyletic clade including

"*Silvestrosaurus*" (Anisian–Ladinian boundary), "*Ceresiosaurus*" (early Ladinian), and *Lariosaurus* (middle to late Ladinian) at the alpha taxonomic level must precede the analysis of phylogenetic interrelationships among its terminal taxa.

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Appendix

The characters listed below are based on the data used previously in the analysis of the phylogenetic interrelationships of *Simosaurus* (Rieppel, 1994a). The data matrix relies heavily on the work of Gauthier et al. (1988), further augmented by the addition of characters taken from Evans (1988) and Storrs (1991, 1993b). Additional references pertaining to the coding of non-sauropterygian taxa can be found in Rieppel (1994a). Coding for the postcranium of *Cymatosaurus* is based on the assumption that *Proneusticosaurus* Volz, 1902, is a subjective junior synonym of *Cymatosaurus* Fritsch, 1894 (Rieppel & Hagdorn, 1996).

1. Premaxillae small (0) or large (1), forming most of snout in front of external nares.

2. Premaxilla without (0) or with (1) postnarial process, excluding maxilla from posterior margin of external naris.

3. Snout unconstricted (0) or constricted (1).

4. temporal region of skull relatively high (0) or strongly depressed (1).

5. Nasals shorter (0) or longer (1) than frontal(s).

6. Nasals not reduced (0), somewhat reduced (1), or strongly reduced or absent (2).

7. Nasals do (0) or do not (1) enter external naris.

8. Nasals meet in dorsomedial suture (0) or are separated from one another by nasal processes of the premaxillae extending back to the frontal bone(s) (1).

9. The lacrimal is present and enters the external naris (0) or remains excluded from the external naris by a contact of maxilla and nasal (1), or the lacrimal is absent (2).

10. The prefrontal and postfrontal are separated by the frontal along the dorsal margin of the orbit (0), or a contact of prefrontal and postfrontal excludes the frontal from the dorsal margin of the orbit (1).

11. Dorsal exposure of prefrontal large (0) or reduced (1).

12. Preorbital and postorbital region of skull: of subequal length (0), preorbital region distinctly longer than postorbital region (1), postorbital region distinctly longer (2).

13. Upper temporal fossa absent (0), present and subequal in size or slightly larger than the orbit (1), present and distinctly larger than orbit (2), or present and distinctly smaller than orbit (3).

14. Frontal(s) paired (0) or fused (1) in the adult.

15. Frontal(s) without (0) or with (1) distinct posterolateral processes.

16. Frontal widely separated from the upper temporal fossa (0), narrowly approaches the upper temporal fossa (1), or enters the anteromedial margin of the upper temporal fossa (2).

17. Parietal(s) paired (0), fused in their posterior part only (1), or fully fused (2) in adult.

18. Pineal foramen close to the middle of the skull table (0), is displaced posteriorly (1), is displaced anteriorly (2), or is absent (3).

19. Parietal skull table broad (0), weakly constricted (1), strongly constricted (at least posteriorly) (2), or forming a sagittal crest (3).

20. Postparietals present (0) or absent (1).

21. Tabular present (0) or absent (1).

22. Supratemporals present (0) or absent (1).

23. The jugal extends anteriorly along the ventral margin of the orbit (0), is restricted to a position behind the orbit but enters the latter's posterior margin (1), or is restricted to a position behind the orbit without reaching the latter's posterior margin (2).

24. The jugal extends backward no farther than to the middle of the cheek region (0), or nearly to the posterior end of the skull (1).

25. The jugal remains excluded from (0) or enters (1) the upper temporal arch.

26. Postfrontal large and plate-like (0), with distinct lateral process overlapping the dorsal tip of the postorbital (1), or postfrontal with reduced lateral process and hence more of an elongate shape (2).

27. Lower temporal fossa absent (0), present and closed ventrally (1), or present but open ventrally (2).

28. Squamosal descends to (0) or remains broadly separated from (1) ventral margin of skull.

29. Quadratojugal present (0) or absent (1).

30. Quandratojugal with (0) or without (1) anterior process.

31. Occiput with paroccipital process forming the lower margin of the posttemporal fossa and extending laterally (0), paroccipital processes trending posteriorly (1), or occiput plate-like with no distinct paroccipital process and with strongly reduced posttemporal fossae (2).

32. Squamosal without (0) or with (1) distinct notch to receive distal tip of paroccipital process.

33. Mandibular articulations approximately at level with occipital condyle (0), displaced to a level distinctly behind occipital condyle (1), or positioned anterior to the occipital condyle (2).

34. Exoccipitals do (0) or do not (1) meet dorsal to the basioccipital condyle.

35. Supraoccipital exposed more or less vertically on occiput (0) or exposed more or less horizontally at posterior end of parietal skull table (1).

36. Occipital crest absent (0) or present (1).

37. Quadrate with straight posterior margin (0) or quadrate shaft deeply excavated (concave) posteriorly (1).

38. Quadrate covered by squamosal and quadratojugal in lateral view (0), or quadrate exposed in lateral view (1).

39. Dorsal wing of epipterygoid broad (0) or narrow (1).

40. Lateral conch on quadrate absent (0) or present (1).

41. Palate kinetic (0) or akinetic (1).

42. Basioccipital tubera free (0) or in complex relation to the pterygoid, as they extend ventrally (1) or laterally (2).

43. Suborbital fenestra absent (0) or present (1).

44. Pterygoid flanges well developed (0) or strongly reduced (1).

45. Premaxillae enter internal naris (0) or are excluded (1).

46. Ectopterygoid present (0) or absent (1).

47. Internal carotid passage enters basicranium (0) or quadrate ramus of pterygoid (1).

48. Retroarticular process of lower jaw absent (0) or present (1).

49. Distinct coronoid process of lower jaw absent (0) or present (1).

50. Surangular without (0) or with (1) strongly projecting lateral ridge defining the insertion area for superficial adductor muscle fibers on the lateral surface of the lower jaw.

51. Mandibular symphysis short (0), somewhat enforced (1), or elongated and "scoop"-like (2).

52. Splenial bone enters the mandibular symphysis (0) or remains excluded therefrom (1).

53. Teeth set in shallow or deep sockets (0) or superficially attached to bone (1).

54. Anterior (premaxillary and dentary) teeth upright (0) or strongly procumbent (1).

55. Premaxillary and anterior dentary fangs absent (0) or present (1).

56. One or two caniniform teeth present (0) or absent (1) on maxilla.

57. The maxillary tooth row is restricted to a level in front of the posterior margin of the orbit (0), or it extends backward to a level below the posterior corner of the orbit and/or the anterior corner of the upper temporal fossa (1), or it extends backward to a level below the anterior one third to one half of the upper temporal fossa (2).

58. Teeth on pterygoid flange present (0) or absent (1).

59. Vertebrae notochordal (0) or non-notochordal (1).

60. Vertebrae amphicoelous (0), platycoelous (1), or other (2).

61. Dorsal intercentra present (0) or absent (1).

62. Cervical intercentra present (0) or absent (1).

63. Cervical centra rounded (0) or keeled (1) ventrally.

64. Zygosphene–zygantrum articulation absent (0) or present (1).

65. Sutural facets receiving the pedicels of the neural arch on the dorsal surface of the centrum in the dorsal region are narrow (0) or expanded into a cruciform or "butterfly-shaped" platform (1).

66. Transverse processes of neural arches of the dorsal region relatively short (0) or distinctly elongated (1).

67. Vertebral centrum distinctly constricted in ventral view (0) or with parallel lateral edges (1).

68. Distal end of transverse processes of dorsal vertebrae not increasing in diameter (0) or distinctly thickened (1).

69. Zygapophyseal pachyostosis absent (0) or present (1).

70. Prezygapophyses and postzygapophyses do not (0) or do (1) show an anteroposterior trend of increasing inclination within the dorsal and sacral region.

71. Cervical ribs without (0) or with (1) a distinct free anterior process.

72. Pachyostosis of dorsal ribs absent (0) or present (1).

73. The number of sacral ribs is two (0), three (1), or four or more (2).

74. Sacral ribs with (0) or without (1) distinct expansion of distal head.

75. Sacral (and caudal) ribs or transverse processes sutured (0) or fused (1) to their respective centrum.

76. Cleithrum present (0) or absent (1).

77. Clavicles broad (0) or narrow (1) medially.

78. Clavicles positioned dorsally (0) or anteroventrally (1) to the interclavicle.

79. Clavicles do not meet in front of the interclavicle (0) or meet in an interdigitating anteromedial suture (1).

80. Clavicles without (0) or with (1) anterolaterally expanded corners.

81. Clavicle applied to the anterior (lateral) (0) or to the medial (1) surface of scapula.

82. Interclavicle rhomboidal (0) or T-shaped (1).

83. Posterior process on (T-shaped) interclavicle elongate (0), short (1), or rudimentary or absent (2).

84. Scapula represented by a broad blade of bone (0) or with a constriction separating a ventral glenoidal portion from a posteriorly directed dorsal wing (1).

85. The dorsal wing or process of the eosauropterygian scapula tapers to a blunt tip (0) or is ventrally expanded at its posterior end (1).

86. Supraglenoid buttress present (0) or absent (1).

87. One (0) or two (1) coracoid ossifications.

88. Coracoid of rounded contours (0), slightly waisted (1), strongly waisted (2), or with expanded medial symphysis (3).

89. Coracoid foramen enclosed by coracoid ossification (0) or between coracoid and scapula (1).

90. Pectoral fenestration absent (0) or present (1).

91. Limbs short and stout (0) or long and slender (1).

92. Humerus rather straight (0) or "curved" (1).

93. Deltopectoral crest well developed (0) or reduced (1).

94. Insertional crest for latissimus dorsi muscle prominent (0) or reduced (1).

95. Humerus with prominent (0) or reduced (1) epicondyles.

96. The ectepicondylar groove is open and notched anteriorly (0), open without anterior notch (1), or closed (2) (i.e., ectepicondylar foramen present).

97. Entepicondylar foramen present (0) or absent (1).

98. Radius shorter than ulna (0), longer than ulna (1), or approximately of the same length (2).

99. Iliac blade well developed (0), reduced but projecting beyond level of posterior margin of acetabular portion of ilium (1), reduced and no longer projecting beyond posterior margin of acetabular portion of ilium (2), or absent (i.e., reduced to simple dorsal stub) (3).

100. Pubis with convex (0) or with concave (1) ventral (medial) margin.

101. Obturator foramen closed (0) or open (1) in adult.

102. Thyroid fenestra absent (0) or present (1).

103. Acetabulum oval (0) or circular (1).

104. Femoral shaft stout and straight (0) or slender and sigmoidally curved (1).

105. Internal trochanter well developed (0) or reduced (1).

106. Intertrochanteric fossa deep (0), distinct but reduced (1), or rudimentary or absent (2).

107. Distal femoral condyles prominent (0) or not projecting markedly beyond shaft (1).

108. Anterior femoral condyle relative to posterior condyle larger and extending farther distally (0) or smaller/equisized and of subequal extent distally (1).

109. The perforating artery passes between astragalus and calcaneum (0) or between the distal heads of tibia and fibula proximal to the astragalus (1).

110. Astragalus without (0) or with (1) a proximal concavity.

111. Calcaneal tuber absent (0) or present (1).

112. Foot short and broad (0) or long and slender (1).

113. Distal tarsal 1 present (0) or absent (1).

114. Distal tarsal 5 present (0) or absent (1).

115. Total number of tarsal ossifications four or more (0), three (1), or two (2).

116. Metatarsal 5 long and slender (0) or distinctly shorter than the other metatarsals and with a broad base (1).

117. Metatarsal 5 straight (0) or "hooked" (1).

118. Mineralized sternum absent (0) or present (1).

119. The medial gastral rib element always only has a single lateral process (0) or may have a two-pronged lateral process (1).

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